UNIVERSITY OF ALBERTA

AGROFORESTRY FOR KENYA: PEST IMPACT AND BIOCONTROL IN A TREE LEGUME-MAIZE INTERCROP

BY

CALLISTUS K. P. O. OGOL

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA

FALL 1996

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ISBN 0-612-18088-3

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NAME OF AUTHOR: **Callistus Kelly Paul Okach Ogol**

TITLE OF THESIS: **Agroforestry for Kenya: Pest Impact and Biocontrol in a Tree Legume-Maize Intercrop**

DEGREE: **Doctor of Philosophy**

YEAR THIS DEGREE GRANTED: **1996**

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Agroforestry for Kenya: Pest Impact and Biocontrol in a Tree Legume-Maize Intercrop** submitted by **Callistus K. P. O. Ogol** in partial fulfillment of the requirements for the degree of **Doctor of Philosophy.**

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DEDICATION

I dedicate this thesis to my wonderful parents Boniface and Rose Ogol,

who took me to school, and made it possible for me to pursue my grandest dream,

and to my wife Lucy, and children Adrian, Esther and Boni,

for their love, support, and endurance.

ACKNOWLEDGMENTS

First and foremost, I wish to thank Dr. John R. Spence my supervisor, for believing and giving me the chance to pursue graduate studies at the University of Alberta, and to conduct my dissertation research in my beloved country, Kenya. I am most grateful for his scholarly guidance, encouragement and support. The warmth of his friendship and care made the many months spent away from my family less painful. I also wish to thank Dr.B.A. Keddie my co-supervisor for his support, guidance, care and friendship. I am most grateful to the other members of my committee; Dr. W.B. Mcgill and Dr. J.A. Volney, for their scholarly advice.

This work could not have been possible without the diligent assistance I received from two research assistants; Peter Omollo Owuor and George Otieno, who spent several tiring days under the scorching tropical sun. Their ability to organize and manage personnel and labour requirements and execute some of the routine scientific procedures while I was shuttling between field sites kept my blood pressure within optimal levels. Peter's acquisition of specific scientific skills and data collection techniques enabled my work to continue for months after my return to Edmonton to embark on my thesis preparation. All the pheromone work was conducted by Samuel Onyango to whom I am most grateful.

I recieved assistance from several people and it may not be possible remembering all of them. I am grateful to Charles Oyugi for planting and taking care of thousands of leucaena seedlingsand for his involvment in the initial stages of my research at Mtwapa. To my good friend Ken Ogedah of ICIPE for his never ending assistance, expertise advice and challenging discussions on various aspects of entomology, and for his unfailing comradeship. To Dr. Bill Overholt and Dr. Slawomir Lux of ICIPE for their generous support and advice. To Dr.Susan Kimani of National Museums of Kenya for assisting with the taxonomy of the parasitoids and unraveling the *Cotesia* mystery, and to Dr. Ed Fuller for assisting with the taxonomy of the Coleoptera. To Dr. D.O. Nyamai of KEFRI for his moral, logistical and scholarly support and encouragement before and during my research.

To my father Boniface Ogol for providing essential transport to Amoyo during some very challenging times. To my wife Lucy for tolerating a husband who was always on the road or away from home for months. To My Children Adrian Esther and Boni for their loyalty and never questioning why *Babu* spent days, weeks and months away from home .....studying bugs? Many fellow graduate students of entomology at the University of Alberta provided unconditional assistance to me during my thesis preparation and wish to thank them all. In particular, I wish to thank Susan Bjornson for her helpful computer skills and for upgrading my computer literacy. To Christian Klingenberg for valuable statistical computer advice and for being a reliable *baada ya kazi* comrade. To Paul Schouten, Jim Hammond and Scott Digweed, all who asisted in various valuable ways.

Finally I wish to thank the Kenya Forestry Research Institute and Kenya Agricultural Research Institute for providing the experimental fields at both Amoyo and Mtwapa respectively. This task could have not been possible without the generous financial support from CIDA/ University of Alberta Scholarship, the African Internship Dissertation Award of theRockefeller Foundation and the African Academy of Sciences, to all of whom I am most grateful.

ABSTRACT

I evaluated the effect of the maize-leucaena agroforestry system on the insect fauna relevant to maize production, to establish if this system has pest management benefits. I also monitored the population dynamics and damage impacts of the leucaena psyllid *Heteropsylla cubana* Crawford, a new arrival to Africa, and carried out faunistic studies on ground-dwelling beetles and spiders. These studies covered six cropping seasons from September 1992 to August 1995, and were conducted at Mtwapa and Amoyo in coastal and western Kenya respectively. Treatments included monocropped and intercropped (maize, leucaena) plots, weeded and unweeded plots, mulched and unmulched plots and, and three spacing regimes for leucaena hedgerows.

I evaluated the resource concentration hypothesis which suggests that herbivores will be less abundant in diverse habitats because non-host species disrupt the ability of the pest to attack its proper host efficiently. Alley cropping leucaena with maize significantly reduced infestation by stem boring lepidopteran pests and their damage to the maize crop, thus supporting the resource concentration hypothesis. Furthermore, the reduced pest numbers translated into increased yields. On the other hand, abundance and activity of the leucaena psyllid and of herbivorous and detrivorous ground-dwelling beetles was unaffected by the cropping system, and did not support the hypothesis.

I also examined possible implications of the enemies hypothesis which posits that vegetational diversity increases both population size and impacts of entomophagous natural enemies that regulate populations of herbivorous arthropod pests. The maize-leucaena cropping system did not increase, and in fact even reduced the abundance and/or activity of some natural enemies of maize stem borers more than in the maize monocrop. The number of ladybirds and ground-dwelling beetles did not differ significantly between treatments. Thus, the enemies hypothesis that natural enemies will be more abundant in polycultures than in monocultures was not corroborated.

Studies on the population dynamics of the psyllid revealed that populations were influenced by weather, particularly rainfall, and availability of suitable shoots. New growth of young shoots following rainfall, encouraged psyllid abundance as long as weather conditions were not extreme. Furthermore, damage to leucaena appeared to represent the cumulative and interactive effect of both the feeding activity of psyllids and prevailing environmental/climatic conditions, and did not closely track the actual population of and/or damage by psyllids at a given time. Psyllid populations were generally much higher at Mtwapa than at Amoyo, suggesting possible environmental constraints on population growth.

The faunistic studies on ground-dwelling beetles and spiders showed a general increase in abundance within plots during the period of these experiments. The two monocrops had consistently lower incidence of both beetles and spiders, while the unweeded plot had highest incidence of spiders, though differences were statistically insignificant. Notwithstanding, my results weakly suggest that vegetational diversity is correlated with abundance of insect populations. Implications of this for biological conservation of arthropods are discussed.

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1. GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1 GENERAL AGRICULTURAL PRACTICES AND ECOLOGY

1.1.1 Agricultural Practices and land degradation

There has been increasing concern about environmental degradation in sub-Saharan Africa and its implications for the ecological future of the continent. Many present agricultural practices lead to soil erosion, water contamination, deforestation, desertification and loss of productivity (Dover and Talbot 1987). These impacts have been aggravated by soils in the tropics, which are commonly highly weathered, low in fertility and, shallow or susceptible to erosion (Jacobson, 1988). Moreover, rapid population growth without corresponding technological developments in agriculture has increased pressure on arable lands throughout tropical Africa (Kerkhof, 1990). The high population growth rate in turn has exacerbated demand for fuelwood and other forest products. Together with recent food shortages and prospects of inadequate supplies in the future, these trends have spurred interest in developing methods for increasing food production in tropical Africa. One such method is multiple cropping, a widespread and centuries-old technique of intensive farming that has persisted in many areas as a method of maximizing land productivity per unit area (Papendick et al., 1976).

1.1.2 Multiple cropping in tropical Africa

Multiple cropping can be described as a range of practices where total production from a unit area of land in a farming year is achieved through growing crops simultaneously, sole crops in sequence, or a combination of mixed and sole crops in sequence (Andrews and Kassam, 1976). Multiple cropping systems are part of traditional farming in Africa (Okigbo and Greenland, 1976). In East Africa, indigenous peasant

farmers responsible for about 90% of food production have always practiced multiple cropping (Abasa, 1983). Throughout the tropics, such farmers have long used crop diversity to minimize the risk of crop failure, improve nutrition and produce high yields of particular crops (Litsinger and Moody, 1976). Several proposals have been offered to explain the increased crop production in multiple cropping, and Perrin (1977) has summarized them into seven: (1) more efficient use of solar radiation due to better interception of light by foliage per unit of space and time, (2) positive interaction between different plant species and mutual or at least unilateral benefits in crop growth and/or reproduction, (3) reduction of the apparent autotoxic effects of certain crops; (4) the more efficient use of soil moisture and nutrients associated with different rooting depths of the constituent crops, (5) maintenance of a dense canopy which smothers weeds and may protect soil from erosion, (6) favourable changes in the incidence of pests and diseases and the significance of their damages, and (7) the potential compensatory growth of these crops in mixtures which suffer least from the vagaries of the environment.

Traditional polycultural farming systems in tropical Africa and other developing nations have undergone changes due to European settlement (and/or colonization) and introduction of European farming techniques which were mainly monocultural with emphasis on cash crops (coffee, tea, sisal, cotton). In many countries, multiple cropping systems were associated with backward peasant farming and were thus discouraged (Beets, 1982). After the second World War, further attempts were made to introduce Western farming techniques into developing countries of the tropics. Some of such attempts were enormous failures due to lack of knowledge and understanding of traditional cropping systems and their socio-economic context (Amoaka - Atta, 1982). Recent research has shown that traditional mixed cropping systems compare favourably with modern techniques. For the tropical small-scale farmer, there was no advantage to be gained by replacing the traditional polycultural practice with monocultural practice (Webster and Wilson, 1966). This had been foreseen as far back as 1934 in Kenya by L.S.B.Leakey (a European settler), who emphasized that more priority should be given to research in indigenous methods of food production than to cash crops because of the

advantages of mixed cropping (Okigbo and Greenland, 1976). Apart from increase in land use efficiency (Francis et al., 1968), polycultures ensure food availability through the season in which short-term crops like pulses are harvested and used while waiting for the longer-term cereals and root crops. For a majority of peasant farmers, monoculture would be both disastrous and unaffordable because of the expensive agrochemicals that go with the system (Abasa, 1983).

1.1.3 Agroforestry as a multiple cropping system

One multiple cropping system that is gaining popularity is agroforestry, an approach that has evolved from the recognition that removal of trees and vegetative cover are among the most important causes of land degradation (Lundgren and Raintree, 1982; Odhiambo, 1990). This has prompted the need for study of management approaches that restore vegetation and at the same time, allow for efficient production of food and fibre. I believe that an agroforestry approach can restore ecological stability and land productivity to a significant part of tropical Africa.

'Agroforestry' is a collective name for land use systems and technologies where woody perennials (trees, shrubs, palms, bamboos, etc.) are grown deliberately on the same land as agricultural crops and/or animals. To qualify as agroforestry, a given land use system or practice must permit significant positive economic and ecological interactions between the different components in order to achieve a more productive and more sustainable and/or more diversified output from the land than is possible with conventional monoculture (Lundgren and Raintree, 1982; Nair, 1984). A wide variety of both traditional, as well as relatively new agricultural systems fall under the umbrella of agroforestry and many of these systems are practiced throughout the tropical and sub-tropical developing nations (Nair, 1984).

Inclusion of woody plants in tropical land use systems offers many advantages at virtually no extra cost. For example, the judicious use of leguminous trees can aid

recycling of plant nutrients and water from the deeper soil profiles, fix nitrogen from the air, intercept fog drip, reduce soil-water evaporation, lower surface temperature, produce woodfuel, produce building materials, provide cash income, and generally increase off-season production to achieve more effective use of land (Douglas, 1972; Kirby, 1976; MacDaniels and Lieberman, 1979; Vietmeyer, 1979; Myers, 1980; National Academy of Sciences, 1980).

Many agroforestry systems have been proposed in recent years. Among these, alley farming is one of the most promising. In this system, arable crops are grown between hedgerows of planted shrubs and trees, preferably leguminous species which are pruned periodically to reduce shading of the intercrop (Kang et al., 1981, 1984). Pruned foliage is allowed to decompose in the alleys and the nutrients released increase the yields of interplanted crops (Kang et al., 1984). The foliage may also be used to provide supplementary fodder to livestock (Sumberg and Okali, 1983). Simultaneously, the trees provide many other by-products such as fuelwood and stems for staking vine crops while also acting to suppress weeds and erosion control (Kang et al., 1989). Alley farming is therefore a low cost, sustainable agricultural technology and an attractive alternative to the prevailing 'shifting cultivation and bush fallow' system practiced by subsistence farmers in sub-Saharan Africa (Swaminathan, 1987).

1.1.4 Plant Diversity and Insect Pest Abundance

Increasing plant diversity, as in agroforestry and other forms of multiple cropping, affect both the diversity (Murdoch et al., 1972; Root, 1973; Price and Waldbauer, 1975) and stability (Pimental., 1961; Southwood and Way, 1970; van Emden and Williams, 1974) of the herbivore community. In multiple cropping, structural and species diversity of vegetation (a measure of the biotic, structural, and microclimatic complexity arising from the mixing of different plants) results from the addition of crop plants in time and space. Low pest population densities over time may reflect greater community stability (Altieri and Liebman, 1986). Modern agricultural practices reduce diversity by promoting

monocultures of single plant species that are genetically and phenologically uniform in time and space (Southwood and Way, 1970; Dempster and Coaker, 1974; Flint and van den Bosch, 1981). Consequently, ecologists have maintained that western agricultural systems, because of their lack of diversity, are inherently unstable and more prone to pest outbreaks (Wilhelm, 1976). Hence, various authors (Perrin, 1977; Perrin and Philips, 1978, Coaker, 1980; Finch, 1980; Cromartie, 1981; Hare, 1983,) have emphasized the potential of managing insect pests by manipulating cropping patterns.

Studies comparing the abundance of specialist herbivores in simple and diverse habitats have documented that monocultures have greater numbers of herbivores than do more diverse habitats (Pimentel 1961; Tahvanianen and Root, 1972; Root, 1973; Dempster and Coaker, 1974; Perrin and Phillips, 1978; Cromartie 1981; Andow, 1983a; Risch et al., 1983; Amoaka-Atta et al., 1983; Ampong -Nyarko et al., 1994). Reductions of pest incidence in diverse vegetation may be the result of a complex of factors like increased parasitoid and predator populations, availability of alternative food for natural enemies, decreased colonization and reproduction of pests, chemical repellency, and masking and /or emigration and optimum synchrony between pests and natural enemies (Matteson et al., 1984). Perrin and Philips (1978) described the stages in pest population development and dynamics that may be affected by mixed cropping. At the crop colonization stage they postulate that disruption of olfactory and visual responses, physical barriers, and diversion of other hosts are important mechanisms regulating herbivores in multiple cropping systems. Once the pest becomes established in the field, populations may be regulated by limitation of dispersal, feeding disruption, reproduction inhibition and mortality imposed by biotic agents.

Vandermeer (1990) summarized the mechanisms believed to operate in reducing pest attack in intercrops in terms of three general hypotheses: (i) *The disruptive-crop hypothesis* (popularly known as 'resource-concentration' hypothesis), largely applicable to specialist herbivores, suggests that non-host species disrupt the ability of a pest to attack its host efficiently. (ii) *The trap-crop hypothesis*, applicable mainly to generalist herbivores, applies where a second species attracts a pest away from the principal species.

(iii) *The enemies hypothesis* suggests that the intercropping situation attracts (for a number of reasons) more predators and parasitoids than monocultures, thus reducing pests through predation or parasitism.

Altieri & Liebman (1986) enumerated seven mechanisms under the resource concentration hypothesis that may interfere with plant host-seeking behaviour and population development. Those that affect host-seeking behavior include: (1) Camouflage, where a host plant is protected from insect pests by the physical presence of other plants; (2) crop background, where certain pests prefer a crop background of a particular colour and/or texture; (3) masking or dilution of attractant stimuli, where the presence of non-host plants mask or dilute the attractant stimuli of host plants leading to a breakdown of orientation, feeding, and reproduction (4) repellent chemical stimuli, where aromatic odours of certain plants disrupt host finding behaviour. The remaining three mechanisms interfere with population development and survival and include: (5) mechanical barriers, in which companion crops may block the dispersal of herbivores across the polyculture, (6) lack of arrestant stimuli causing a herbivore landing on a non-host to leave the plot quickly and, (7) microclimatic influences, in which, favourable aspects of microclimate conditions are highly fractioned, making the system and therefore insects experience difficulty in locating and remaining in suitable microhabitats.

Although assertive responses to the foregoing ecological phenomenon have been reported for several insect pest species, exceptions to the general rule that 'crop diversity is associated with reduced pest populations' have been documented, and that the outcome may vary enormously among plant combinations (Kareiva, 1983). Ehrlich et al. (1977) argued that merely adding more plant species to agricultural ecosystems will not necessarily stabilize them and may even have exactly the opposite effect. An examination of 198 herbivore species on the effects of multiple cropping on their populations revealed that 53 percent exhibited lower abundance in multicrops than in monocultures, 18 percent were more abundant in multicrops, 9 percent showed no difference and 20 percent showed a variable response (Andow, 1983b; Risch et al., 1983). More recent reviews of literature (Andow, 1986, 1988) showed that 56% of herbivores had lower population densities,

16% had higher, and 28% had similar or variable densities in polycultures compared with monocultures, affirming that diversity does not always lead to reduction in pest numbers.

It is apparent that there is no general theory from which to predict optimal crop associations. This requires that specific proposals must be tested in well designed field experiments (Huffaker, 1982; Herzog et al., 1984). Therefore, detailed entomological studies on specific cropping systems are necessary to establish the structure of the system and how they could be manipulated for purposes of pest management. To date, few studies of this nature have been reported for agroforestry systems, and before significant investment and land base conversion occurs, there is an urgent need for such studies.

1.2 THE LEUCAENA -MAIZE SYSTEM

1.2.1 Maize, its history and importance in tropical Africa

Maize is not indigenous to Africa and archeological evidence indicates that it originated and was first used as a crop in Central America and the Andean Region in South America (Rundquist, 1984). According to Miracle (1966), maize was probably introduced to Africa at more than one point and at different times. Even though the Portuguese may have been the first to introduce it to the African continent, it is unlikely that they were responsible for all introductions. Linguistic evidence suggest that many areas of northern tropical Africa received maize across the Sahara, and Arab traders may also have introduced it to other areas (Miracle, 1966). Maize was first introduced in East Africa by Portuguese traders in the sixteenth and seventeenth centuries (Acland, 1971). Its cultivation was limited to coastal areas up to the end of the nineteenth and the beginning of the twentieth centuries when white settlers introduced new varieties better suited to the inland climate (Acland, 1971). From then onwards maize spread very quickly among the African population and has grown to be the most important staple food crop (Gerhart, 1975; Rundquist, 1984; Ampofo, 1988).

In Kenya, almost half the acreage used for food crops in the small farm sector is planted to maize (Rundquist, 1984). More than 1 million hectares of maize with a production of 1.4 million tons are cultivated. Large scale farms produce 13% of the total production on 10% of the area and supply 45% of the maize sold in local markets. The remaining 87% of the Kenyan maize production is used by the farming population and only a small surplus is marketed for profit (Dissemond and Hindorf, 1990). It is the basic foodstuff for about 90% of the population (Gerhart, 1975).

1.2.2 Leucaena: history and uses in tropical Africa

Leucaena is a genus of the family Leguminoseae, and while botanical literature of the past 2 centuries contains claims for 51 species within this genus, 10 species were recognized as valid a decade ago (Brewbaker et al., 1972), to which another two were later added (Leucaena Research Reports (LRR)7(2):7-20). Recently, about 15 species have been reported (ICRAF, 1993). Of the various species, only *Leucaena leucocephala* (Lam.) de Wit has been exploited extensively, with the universally used common name of 'leucaena' (NAS, 1977). Depending on variety, leucaena is either a tall, slender tree that may grow up to 20 m, or a rounded, many branched shrub less than 5 m high. It has feathery leaves, bunches of long, brown pods and small, white 'powderpuff' flowers (NAS, 1980).

Leucaena is a perennial tree that originated in Mexico. Some varieties were spread widely throughout the region thousands of years ago by the Maya and Zapotec civilizations (NAS, 1977). In 1565, after the conquest of Mexico, the Spanish conquistadors organized trade with the Philippines and sometime during the 250 years that this continued, leucaena reached the Philippines, probably carried as forage (NAS, 1977). Because of its desirable qualities, it was introduced to plantations in the Netherlands East Indies (now Indonesia), Papua New Guinea, Malaya (Malaysia), and other countries in southeastern Asia (NAS, 1977). During the nineteenth century, it was taken to Hawaii,

Fiji, northern Australia, India, East and West Africa, and the islands of the Caribbean, and is now truly pantropical (NAS, 1977).

Of all tropical legumes, leucaena probably offers the widest assortment of uses which include the following: forage, firewood, timber, and organic fertilizer. Its ability to thrive on steep slopes, in marginal soils and in areas with an extended dry season makes it a prime candidate for restoring forest cover to watersheds, slopes, and grasslands that have been denuded through deforestation or fire (NAS, 1977, 1980). Due to its fast growth and rapid regeneration time, adaptation to a wide range of soils and relative ease of establishment and other beneficial qualities, leucaena has spread widely across tropical Africa. In most government research stations in eastern and southern Africa (e.g. Kenya, Tanzania, Zambia, Uganda, Zimbabwe, etc.), leucaena plantings dating back to the late 1960's can be found (Otsyina and Dwodzela, 1995). The same is true of other parts of Africa and presently, leucaena is being used extensively for various products and services in Africa (NAS, 1980,1984). Its uses in Africa include; fodder production, fuelwood, construction wood, soil fertility improvement, and soil conservation (Otsyina and Dwodzela, 1995).

A number of reports on when leucaena was introduced to various East African countries are available in the literature. In Burundi, it was first introduced from Yangambi, Zaire in 1933 and its use was limited to providing shade to coffee plantations, but from the 1980's, was recognized as high quality fodder for livestock and has gained the interest of forage management scientists. (Ndayiragije and Salvator, 1995). In Mozambique, plantations were first established in 1977 and the tree is mainly used for fuelwood, fodder and soil fertilization (da Silva Raus and da Trindade Mário Rombe, 1995). In Malawi, there are unconfirmed reports that attempts to introduce (though unsuccessfully) leucaena were made as early as 1891 when the first government botanist, Alexander Whyte, planted a couple of trees in the first Botanic Garden in central Africa (Edwards and Darwin, 1983). However, it was probably in 1969 that the first successful plantings of leucaena were made at the Bunda College of Agriculture as a fodder crop. It has now spread almost throughout the country where farmers grow it for various purposes including soil and

yield improvement, animal feed, shade and windbreak, soil protection, fuelwood and polewood (Chilima et al., 1995). In Mauritius, leucaena is locally known as 'acacia' and was introduced in 1767 by Pierre Poivre. It is mainly found in dry lowlands near the coast and grows in the wild in association with other plant species. In Rodrigues, a dependency of Mauritius, leucaena is widespread throughout the island and is used mainly as fodder for livestock production, as windbreaks in orchards and in erosion control (Rawanawshah, 1995). In Ethiopia, leucaena was probably first introduced in 1979 at a place called Bako, some 250 km west of Addis Ababa for the purpose of producing animal browse. Though conditions such as high altitude and acid soils has limited its spread, there are suitable pockets of land where the species can be grown successfully. It has become popular in both rural and urban areas due to its importance in alleviating fodder shortage, low soil fertility and lack of fuelwood (Azage, 1995). In Uganda, leucaena is a recently introduced agroforestry tree species following a farm forestry project funded by DANIDA and implemented by CARE 1984-1990. It is now widespread and used as fuel wood, fodder, organic fertilizer, and revegetation of hillsides among other uses (Maiteki et al., 1995). In Zambia, the early plantings of leucaena date back to the 1970's in a small farm in Lundazi, Eastern province. The tree is now established except in the Northern Province and is fulfilling a number of agroforestry needs, particularly soil improvement and stabilization, fodder, fuelwood, covercrop for agricultural crops and timber requirements (Shakacite, 1995).

I have been unable to determine exactly when leucaena was first introduced to Kenya. The earliest reference available in the literature is by Dale and Greenway (1961) who described *Leucaena glauca* (L.) Benth (Mimosaceae) as 'an unarmed tropical American, small tree with bipinnate, somewhat glaucous leaves, heads of white flowers and pods to 7 inches long', and went on to say that it 'has been widely used in agriculture and has become naturalized in places along the coast'. However, it is widely acknowledged that only *Leucaena leucocephala* has been exploited extensively, and that it has been recorded in the literature under several incorrect names or synonyms, including

L. glauca (NAS, 1977). *L. glauca* is not listed as a species in the current literature, suggesting that the authors could have been referring to *L. leucocephala.*

Even though there is no reliable estimate of the area planted with leucaena in Kenya, it is planted as fodder wherever dairy cattle are reared by zero grazing, and pockets exist along the coast, in the central highlands and in western Kenya (Rao, 1995). Presently, leucaena has attracted considerable scientific attention from Kenyan based international and local research institutions like the International Centre for Research in Agroforestry (ICRAF), Kenya Forestry Research Institute (KEFRI) and Kenya Agricultural Research Institute (KARI), and many research trials involving leucaena are found on -station and on-farm, the latter involving local participating farmers. Consequently, some farmers have fully adopted agroforestry practices that evolve around the use of leucaena (Gichora and Odera, 1995). In addition, several international and local non-governmental organizations as well as government departments have been involved in agroforestry extension activities in various parts of the country that include the use of leucaena. Thus, leucaena is probably the best known multipurpose tree species among the Kenyan community involved in any form of agroforestry practices.

In general, leucaena has been used extensively in agroforestry in Africa in the last two decades. It is adapted widely to the humid and sub-humid regions of eastern and central Africa, the southern African plateau, the humid lowlands of west Africa and even semi-arid regions wherever adequate moisture is available (Rao, 1995). Although the potential of leucaena to provide a wide assortment of products is well acknowledged, its use and integration into African farming systems has been limited by several technological, bio-physical and socio-economic factors including lack of appropriate and proven technologies, poor adaptation to acid soils and high altitudes, and pests (Otsyina & Dwodzela, 1995).

1.2.3 Why leucaena - maize?

The productivity of cereals like maize is heavily dependent on the supply of nitrogen from the soil (Mureithi et al., 1994). In Kenya, maize varieties producing 1700kg to 5500kg/hactare of grain usually remove 36-140 kg/hactare of nitrogen (Arnon, 1975). However, most soils cannot supply more than 20-25% of nitrogen required by maize (Prasad, 1978), and soon, the ability of such soils to support plant growth is diminished. Thus, in places like coastal Kenya, maize production is often limited by nitrogen deficiency (Goldson, 1970, Mureithi et al., 1994), and the application of fertilizers is nearly always necessary. However, most subsistence farmers in tropical Africa cannot afford the expensive fertilizers required for continuous and sustainable production. Consequently, alternative farming methods like agroforestry, are being investigated as a means of ameliorating the problems associated with nutrient deficiency in maize agroecosystems.

The concept of alley-cropping, or hedgerow intercropping is currently being evaluated in many parts of the tropics. Many such studies have involved field trials with leucaena and maize, and results of some have been published (Kang and Duguma, 1985; Mureithi et al., 1994). Higher maize yields have been reported when it is alley cropped with leucaena. Moreover, large savings in nitrogen fertilizer have been achieved when maize is alley cropped with leucaena (Ngambeki, 1985). With respect to yield sustainability, long term observations on sandy soils have reported significantly higher maize yields when it is alley cropped with leucaena than when grown in monoculture with or without applied nitrogen. These positive results seem to reflect mainly improved soil properties (Kang and Duguma, 1985).

Considering the limited resources available to the traditional, resource and technology limited subsistence farmers in tropical Africa, low input, regenerative and/or sustainable production systems as have been demonstrated in the alley cropping of maize and leucaena deserve greater scientific attention. The need to fully understand all bio-physical and socio-economic interactions within this system cannot be overemphasized.

This is crucial considering the generally important role maize plays in the local nutrition and economies of the peoples of tropical Africa.

1.2.4 Pests of maize and their history

Over 30 insect species and species complexes are known to damage maize plants in eastern and southern Africa. However, only seven; *Buseola fusca* Fuller (Lepidoptera: Noctuidae), *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae), *Sesamia calamistis* (Hampson) (Lepidoptera: Noctuidae), *Eldana saccharina* (Walker) (Lepidoptera: Pyralidae), *Cicadulina* spp. (Homoptera: Cicadellidae), *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae) and termites are consistently reported to cause economic damage (Ingram, 1958; Nye 1960; Mathez, 1972; Sheshu Reddy, 1983; Ampofo, 1988). An additional species, *Chilo orichalcociliellus* Strand (Lepidoptera: Pyralidae), is economically important at the east African coast (Sheshu Reddy, 1983, Hill, 1994).

Five of the above, (*C. partellus, C. orichalcociliellus, B. fusca, E. saccharina* and *S. calamistis*) are stem borers (Sheshu Reddy, 1983). Of these, the introduced stem borer, *C. partellus* is generally considered to be the most economically important pest of maize and sorghum in East Africa, at elevations below 1500m (Ingram, 1958; Skoroszewski and van Hamburg, 1987; Greathead, 1990; Sheshu Reddy, 1991). It is indigenous to the southeastern and southern parts of Asia (Päts, 1992). The first record of *C. partellus* in Africa was from Malawi (then Nyasaland) in 1932 (Jepson, 1954). Thereafter, it was recorded in Uganda in 1953 (Ingram, 1958) and in South Africa in 1958 (van Hamburg, 1979). It is now found in most of the lowland areas (<1500 m) of the eastern and southern parts of Africa (CAB, 1989), and is likely to spread further.

Chilo partellus moths emerging from old stubble and wild hosts colonize newly planted maize soon after plant emergence (Päts and Wiktelius, 1992). Plant injury is caused by larval feeding in the plant whorl and later through stem tunneling (Overholt, 1994). Grain losses ranging from 24-36% in maize have been reported (Chatterji et al.,

1969). However, effective chemical control of stem borers is both difficult and costly because they cause damage inside stalks where they are protected, are present in the field throughout the cropping season, and have a number of alternative hosts. There is an urgent need to address and seek pest management strategies for stem borers that are economically feasible and ecologically sustainable for the tropical African maize farmer.

1.2.5 Pests of leucaena and their history

Generally, leucaena shows high resistance to insect pests and insect damage is uncommon except to pods and seed (Pound and Martinez Cairo, 1983). However, two insects have been known to cause severe damage to leucaena trees over the last 15 years: termites and psyllids. Termites make it virtually impossible to establish leucaena without pesticide use in some areas such as East Africa (Brewbaker, 1987). For example, in Malawi, termites attack young seedlings, which must be treated with insecticide, or planted in extra numbers at the outset (NAS, 1977).

The leucaena psyllid, *Heteropsylla cubana* Crawford (Homoptera: Psyllidae), was first described in 1914, but remained unknown and was not a serious pest in its native range of Latin America due to heavy predation and parasitization (Proverbs, 1985). However, in 1980, it was observed attacking leucaena in the Dominican Republic (Brewbaker, 1987) and in Florida (USA) in 1983 (LRR 5:86). This was immediately followed by its discovery in Hawaii, USA in April 1984 (LRR 5:91), in the South Pacific in 1985 and in S.E Asia and Australia in 1986 (LRR 7:6). The invasion of the leucaena psyllid in the Asia-Pacific region affected the multi-purpose tree species (MPTS) projects underway in the region to such an extent that it stimulated two major international workshops, one in Molokai, Hawaii in November 1986 (NFTA, 1987), and another in Bogor, Indonesia in January 1989 (Napompeth and MacDicken, 1990). In addition, several workshops, seminars and conferences were organized independently at the national level in countries such as Indonesia, Philippines and Thailand (Napompeth, 1995).

The psyllid then crossed over to Africa where it was first discovered off the African coast in the Indian ocean island of Mauritius in October 1991 (Rawanawshah, 1995), and Reunion island in November, 1991 (Hollis, 1992). Soon after, it was reported in Madagascar in March 1992 (Reynolds and Bimbuzi, 1992), on the coast of Tanzania and Kenya in July-August 1992 (Reynolds and Bimbuzi, 1992), Burundi in June 1993 (Rao, 1995), Uganda in June-August 1993 (Rao, 1995), Ethiopia in September 1993 (Azage, 1995), Malawi in November 1993 (Rao, 1995), Mozambique sometime in 1993 (da Silva Raus and da Trindade Mário Rombe, 1995) and Zambia in February, 1994 (Shakacite, 1995). It is still spreading. Thus, in just over 10 years, the psyllid has spread from its native range in Mexico and central America, across the Pacific islands to Asia, and across the Indian ocean to Africa (Table 1.1).

The mode of introduction and means of dispersal of *H. cubana* still remain a puzzle. According to Waage (1990), the meteorological calculations and methods developed to study the dispersal of the rice brown plant hopper *Nilaparvata lugens* indicate that its dispersal to Hawaii and subsequently from Hawaii to Guam and Samoa was certainly aircraft assisted. Dispersal through southeast Asia, Australia and into Sri Lanka and India was probably due to its being carried by monsoon wind. He concluded that dispersal of *H. cubana* by monsoon wind into Africa would be difficult.

According to Napompeth (1995), both nymphs and adults of the psyllid suck sap from leucaena terminal shoots. Young flowers are also infested but less frequently. The older leaves are in most cases not attacked. Feeding results in terminal shoots which may become desiccated and consequently, growth is stunted. High psyllid populations produce copious amounts of honeydew which gives rise to the development of sticky black sooty mould coating terminal shoots and leaflets. In heavy infestations, complete defoliation is common. Although plants recover in most cases, death of damaged plants has been known to occur.

The future use of leucaena in African agroforestry systems, though threatened by the psyllid, may be ensured through research. Research by scientists in Asia, Australia and

Table1.1: Progressive invasion and spread of leucaena psyllid between 1980 and 1994

Year	Countries invaded	Reference
1980	Dominican Republic	Brewbaker, 1987
1983	Florida, USA	LRR,* 5:86
1984	Hawaii, USA	LRR, 5:91
1985	Guam, Saipan, Cook Island, Western Samoa, Tahiti, Tonga, Fiji, Solomon islands, Christmas Island, New Caledonia, Papua New Guinea, Okinawa, Taiwan, Philippines	FAO, 1994 Napompeth, 1995
1986	Honkong, Macao, southern China Thailand, Laos, Vietnam, Cambodia, southern Mynamar Malaysia, Singapore, Indonesia	FAO, 1994 Napompeth, 1995
1987	Southern India	FAO, 1994
1991	Western India, Reunion, Mauritius	FAO, 1994; Hollis, 1992; Rawanawshah, 1995
1992	Madagascar, Tanzania, Uganda	Reynolds and Bimbuzi, 1992
1993	Uganda, Burundi, Malawi, Ethiopia, Mozambique	Rao, 1995; Azage, 1995 da Silva Raus & da Trinidade Mário Rombe, 1995
1994	Zambia	Shakacite, 1995

*LRR = Leucaena Research Reports.

Pacific Islands, where the insect has been present for several years, and in Mexico and Central America, the native habitats for both leucaena and the psyllid, has led to the development of pest management tactics that have potential use and adoption in Africa. Consequently, many of the recommendations of the international workshop on management of the leucaena psyllid held in Bongor, Indonesia are considered valid for African countries (FAO, 1994; Napompeth, 1995). They include (1) the identification and testing of psyllid resistant tree composites, (2) development of a biological control capacity, (3) identification of indigenous natural enemies of the psyllid and factors that regulate their populations, (4) introduction of known exotic natural enemies, and (5) monitoring psyllid populations. A regional workshop to set these goals in an African context was held in Dar-es-Salaam, Tanzania in October 1994 (Ciesla and Nshubemuki, 1995).

1.3 OBJECTIVES OF STUDY

My studies as reported in this thesis, were aimed at the maize-leucaena agroforestry system in Kenya with the main objectives of (1) evaluating the effect of this production system on the insect fauna relevant to crop production, and (2) establishing if this system has pest management potential. The work was conceptualized around two general hypotheses, the resource concentration hypothesis and the enemies hypothesis, both of which have been variously proposed to be responsible for lower abundance of insect pests in polycultures than in monocultures.

Chapter 2 examines the role of resource concentration on populations of insect pests of maize in maize-leucaena alley cropping systems. It attempts to establish whether this production system had any effect on host finding, colonizing ability, and abundance of stem boring lepidopterans. Furthermore, I compared the damage levels and yield losses caused to maize by these pests between monocultures and several variations on the alley cropping arrangement.

Chapter 3 examines the role and impact of the enemies hypothesis on stem-boring insect pests of maize in the maize-leucaena agroforestry system. It provides information about the abundance and activity of natural enemy populations of the lepidopteran pests of maize in various cropping treatments and establishes whether the enemies hypothesis applies in this agroforestry system.

Chapter 4 reports on the abundance of the leucaena psyllid, in the context of both the resource concentration and the enemies hypotheses. Seasonal population dynamics of the psyllid is described at two sites in relation to local weather conditions. Possible effects on generalist natural enemies (ladybird beetles) are examined, and the level of damage caused to leucaena plants by psyllid populations is compared among alley cropping treatments.

Chapter 5 reports on the ground-dwelling beetle and spider populations within the cropping systems in the context of both the resource concentration and the enemies hypotheses. The potential of agroforestry systems for the conservation of tropical arthropods is discussed.

1.4 REFERENCES

Abasa, R. O. 1983. Current and future pest management studies in polycultural systems in East Africa. Insect Sci. Application Vol. 4, No. 1/2 pp. 167-171.

Acland, J. D. (1971). East African Crops. An introduction to the production of field and plantation crops in Kenya, Tanzania and Uganda. Longman, FAO. Singapore.

Altieri, M. A. & M. Liebman. 1986. Insect, weed, and plant disease management in multiple cropping systems, pp. 183-218. *In* C.A. Francis [ed.], Multiple cropping systems. Macmillan, London.

Amoaka - Atta, B. 1982. Intercropping. A case study on the stem/pod borer interactions with maize cowpea sorghum cropping patterns in Kenya. ICIPE, pp.123.

Amoaka -Atta, B., E. O. Omolo and E. K. Kidega. 1983. Influence of cowpea and sorghum intercropping systems on stem-/pod-borer infestations. Insect Sci. Application Vol. 4, No. 1/2, pp. 47-57.

Ampofo, J. K. O. 1988. Assessment of On-Farm Losses in Maize Production Due to Insect Pests. Insect Sci. Application Vol. 9, N0. 6, pp., 687-690.

Ampong-Nyarko, K. V. Sheshu Reddy, R. A. Nyangor and K. N. Saxena. 1994. Reduction of insect pest attack on sorghum and cowpea by intercropping. Entomol. exp. appl. 70: 179-184.

Andow, D. A. 1983a. The extent of monocultures on insect populations with particular reference to wheat and cotton. Agric.Ecosyst. Envt. 9: 25-35.

Andow, D. A. 1983 b. Plant diversity and insect populations in experimental agroecosystems: interactions among beans, insects and weeds. Ph.D. dissertation, Cornell University, Ithaca, N.Y.

Andow, D. A. 1986. Plant diversification and insect population control in agroecosystems. *In.* D. Pimentel [ed.], Some aspects of integrated pest management. Dept. Entomology, Cornell University, Ithaca, N.Y. pp. 277-386.

Andow, D. A. 1988. Management of weeds for insect manipulation in agroecosystems. *In* M. A Altieri & M. Liebman, [ed.], Weed management in agroecosystems: ecological approaches. CRC, Boca Raton, Fla. pp. 265-301.

Andrews, D. J. & A. H. Kassam. 1976. The importance of multiple cropping in increasing world food supplies. *In* Multiple Cropping. American Society of Agronomy, Special Publication No. 27, pp.1-10.

Arnon, L. 1975. Mineral nutrition of maize. Int. Potash. Inst., Berne, Switzerland. pp. 452.

Azage, T. 1995. Leucaena and leucaena psyllid in Ethiopia. *In* Ciesla, W. M. and L. Nshubemuki, (eds.), Leucaena Psyllid: a threat to agroforestry in Africa. Proceedings of a Workshop, 10-24 October, Dar-es-Salaam, United Republic of Tanzania. FAO, pp. 99-102.

Beets, W. C. 1982. Multiple Cropping and Tropical Farming Systems. Westview Press Inc., Boulder, Colorado. 156 pp.

Brewbaker, J. L. 1987. *Leucaena*: a multipurpose tree genus for tropical agroforestry. *In* H. A.Steppler and P.K.R. Nair, (eds.), Agroforestry a decade of development, ICRAF, Nairobi, Kenya, pp. 289-323.

Brewbaker, J. L. , D. L. Plucknett and V. Gonzalez. 1972. Varietal variation and yield trials of *Leucaena leucocephala* (koa hoale) in Hawaii. Hawaii Agricultural Experiment Station Bulletin No. 166. University of Hawaii, College of Tropical Agriculture, Honolulu. 29 pp.

C.A.B. 1989. Distribution maps of pests. Series A, Map No. 184. Int.Inst.Ent., London.

Chatterji, S. M., W.R. Young, G. C. Sharma, I. V. Sayi, B. S. Chahal, Y. S. Rathore, V. P. S. Panwar and K. H. Siddiqui. 1969. Estimation of loss in yield of maize due to insect pests with special reference to borers. Ind. J. Entomol. 31: 109-115.

Chilima, C. Z. ,G. S. Meke, L. A. Sitaubi and C. Coote, 1995. The status of leucaena and leucaena psyllid in Malawi. *In* Ciesla, W.M. and L. Nshubemuki, (eds.), Leucaena Psyllid: a threat to agroforestry in Africa. Proceedings of a Workshop, 10-24 October, Dar-es-Salaam, United Republic of Tanzania. FAO, pp. 72-77.

Ciesla, W.M. and L. Nshubemuki (eds.), Leucaena Psyllid: a threat to agroforestry in Africa. Proceedings of a Workshop, 10-24 October, Dar-es-Salaam, United Republic of Tanzania. FAO.

Coaker, T.H. 1980. Insect pest management in Brassica crops by intercropping. I.O.B.B.W.P.R.S. Bull., 3: 117-125.

Cromartie, W. J. 1981. The environmental control of insects using crop diversity. *In* D. Pimentel (ed.), Handbook of Pest Management in Agriculture, vol. 11, CRC Press, Boca Raton. FL, pp. 223-251.

Dale, I. and Greenway, P. J. 1961. Kenya Trees and Shrubs. Buchanan's Kenya Estates Ltd. Nairobi, Kenya. 654 pp.

da Silva Raus, C. E and R. M da Trindade Mário Rombe. 1995. Preliminary observations on Leucaena development in Mozambique. *In* Ciesla, W.M. and L. Nshubemuki, (eds.), Leucaena Psyllid: a threat to agroforestry in Africa. Proceedings of a Workshop, 10-24 October, Dar-es-Salaam, United Republic of Tanzania. FAO, pp. 58-66.

Dempster, J. P. and T. H. Coaker. 1974. Diversification of crop ecosystem as a means of controlling pests. *In* D. P. Jones and M. E. Solomon, (eds.), Biology in Pest and Disease Control. Wiley, New York, pp. 106-114.

Dissemond, A. and H. Hindorf. 1990. Influence of sorghum/maize/cowpea intercropping on the insect situation at Mbita/Kenya. J. Appl. Entomol. 109: 144-150.

Dover, M. and L. Talbot. 1987. To Feed the Earth - AgroEcology for Sustainability in a Changing World Order. World Resources institute, 122 pp.

Douglas, J. S. 1972. Tree crops for forage and cash. World crops, January/February, pp. 15-19.

Edwards, I. and T. Darwin. 1983. Trees, shrubs and woody climbers of Zomba Botanical Garden. Research Record 61, FRIM, Zomba.

Ehrlich, P. R., A.H. Ehrlich and J. P. Holdren. 1977. Ecoscience: Populations, Resources, Environment. Freeman, New York, 1051pp.

FAO (Food and Agriculture Organization). 1994. Leucaena psyllid in the Asia-Pacific region: Implications for its management in Africa. RAPA Publication: 1994/13, FAO Regional Office for Asia and the Pacific (RAPA), Bankok, Thailand. 27pp.

Finch, S. 1980. Chemical attraction of plant-feeding insects of plants. Appl. Biol. 5: 67-143.

Flint, M. L. and van der Bosch. 1981. Introduction to Integrated Pest Management. Plenum, New York, 240pp.

Francis, C.A., C.A. Flor and M. Prager. 1968. Effects of bean association on yield and yield components of maize. Crop. Sci. 18: 760-764.

Gerhart, J. D. 1975. The Diffusion of Hybrid Maize in Western Kenya. Abridged by CIMMYT - Centro Internacional de Mejorament de Maiz y Trigo. Mexico City.

Gichora, M. and J. Odera. 1995. The status of leucaena Psyllid in Kenya. *In* Ciesla, W.M. and L. Nshubemuki, (eds.), Leucaena Psyllid: a threat to agroforestry in Africa. Proceedings of a Workshop, 10-24 October, Dar-es-Salaam, United Republic of Tanzania. FAO, pp. 67-71.

Goldson, J.R. 1970. Coast agriculture and its future in Kenya. World crops 22: 330-331.

Greathead, D. J. 1990. Utilization of natural enemies of *Chilo* spp. for management in Africa. Insect Sci. and its Application 11: 749-755.

Hare, J. D. 1983. Manipulation of host suitability for herbivore pest management. *In* R. F Denno and M. S. Mclure, (eds.), Variable plants and herbivores in natural and managed systems. Academic Press, New York, pp. 655-680.

Herzog, D. C., J. L. Stimac, D. G. Boucias and V. H. Waddill. 1984. Compatibility of biological control in soybean insect management. *In* P. L. Adkisson and Shijun Ma (eds.), Proceeding of the Chinese Academy of Sciences -US National Academy of Sciences joint Symposium in Biological Control of insects. September 25-28 Beijing, China, Science Press. Beijing, Peoples Republic of China, pp. 37-60.

Hill, D.S. 1994. Agricultural Entomology. Timber Press. Portland, Oregon. 635pp.

Hollis, D. 1992. Leucaena psyllid, *Heteropsylla cubana* Crawford newly recorded in Mauritius and Reunion. FAO plant Protection Bulletin 40 (1-2): 49 - 50.

Huffaker, C. B. 1982. Overall approach to insect problems in Agriculture. *In* J. L. Hatfield and I. J. Thomasen, (eds.), Biometeorology in Integrated Pest Management. Academic Press, New York, pp.171-192.

ICRAF. 1993. Annual Report 1993. International Centre for Research in Agroforestry. ICRAF, Nairobi, Kenya. 208 pp.

Ingram,W. R. 1958. The lepidopterous stalk-borers associated with Graminae in Uganda. Bull. Ent. Res. 49: 367-383.

Jacobson, J. L. 1988. Environmental Refugees Yardstick of Habitability. Worldwatch Paper No. 86. Worldwatch Institute, Washington DC, 88pp.

Jepson, W. F. 1954. A critical review of the world literature on the lepidopterous stalk borers of tropical graminaceous crops. Commonw. Inst. Ent., London, 127 pp.

Kang, B. T. and B. Duguma. 1985. Nitrogen management in alley cropping systems. *In* B.T. Kang and J.van der Heide, (eds.) Nitrogen in farming systems in the humid and sub-humid tropics. Haren, Netherlands: Institute of soil fertility.

Kang, B. T. , G.F. Wilson and L. Sipkens. 1981. Alley cropping maize (*Zea mays*) and Leucaena (*Leucaena leucocephala* Lam) in southern Nigeria. Plant and Soil, 63: 165-179.

Kang, B. T. , G. F. Wilson and T.L. Lawson. 1984. Alley cropping: a stable alternative to shifting cultivation. IITA, Ibadan, Nigeria. 22pp.

Kang, B. T., A. C. B. M. van der Kruijs and D. C. Cooper. 1989. Alley cropping for food production in the humid and subhumid tropics. *In* Kang, B. T., and Reynolds, L. (eds.), Alley Farming in the Humid and Subhumid Tropics, pp. 16-26. International Development Research Centre, Ottawa, Canada.

Kareiva, P. M. 1983. Patchiness, dispersal and species interactions: Consequences for communities of herbivore insects. *In.* J. Diamond and T.Case (eds.), Community ecology, Harper and Row, New York, pp.192-206.

Kerkhof, P. 1990. Agroforestry in Africa: A survey of project experience. Panos Publications Ltd., London, U.K. 216 pp.

Kirby, J. M. 1976. Forest grazing: a technique for the tropics. World crops. Nov/Sec, pp 242-251.

Litsinger, J. A., and K. Moody. 1976. Integrated pest management in multiple cropping systems, pp. 293-317. *In* R. I. Papendick, P. A. Sanchez, and G. B. Triplett, [ed.], Multiple cropping. Am. Soc. Agron. Madison, Wisc.

Lundgren, B. O. and J. B. Raintree. 1982. Sustained agroforestry. *In* B. Nestel, (eds.), Agricultural research for development: Potentials and challenges in Asia. ISNAR, The Hague, pp. 37-49.

MacDaniels, L. H. and A. S. Lieberman. 1979. Tree crops: a neglected source of food and forage for marginal lands. Bioscience 29: 173-175.

Maiteki, G., P. Kiwuso and W. Kigenyi. 1995. Leucaena Psyllid a threat to agroforestry in Africa: Uganda's case. *In* Ciesla, W.M. and L. Nshubemuki, (eds.), Leucaena Psyllid: a threat to agroforestry in Africa. Proceedings of a Workshop, 10-24 October, Dar-es-Salaam, United Republic of Tanzania. FAO, pp. 103-106.

Mathez, F. C. 1972. *Chilo partellus* Swinh.; *C. orichalcociliellus* Strand (Lepidoptera: Crambidae) and *Sesamia calamistis* Hmps (Lepidoptera: Noctuidae) on maize in the Coast Province, Kenya. Mitt. schweiz ent. Ges. 45, 267-289.

Matteson, P. C., M. A. Altieri and W. C. Gagne. 1984. Modification of smaller farmer practices for better management. Annu. Rev. Entomol. 29: 383-402.

Miracle, M. P. 1966. Maize in Tropical Africa. The University of Wisconsin Press, Madison, Wisconsin, 327pp.

Murdoch, W. M., F. C. Evans and C. H. Peterson. 1972. Diversity and pattern in plants and insects. Ecology 53: 819-829.

Mureithi, J. G., R. S. Tayler and W. Thorpe. 1994. The effects of alley cropping with *Leucaena leucocephala* and of different management practices in the productivity of maize and soil chemical properties in lowland coastal Kenya. Agroforestry Systems 27: 31-51.

Myers, N. 1980. The conversion of tropical forests. Environment 22: 6-13

Nair, P. K. R. 1984. Soil productivity aspects of agroforestry. International Council for Research in Agroforestry, Nairobi, Kenya.

NAS. 1977. Leucaena: Promising Forage and Tree Crop for the Tropics. National Academy of Sciences, Washington, D.C. 115pp.

NAS. 1980. Firewood Crops: shrubs and tree species for energy production. National Academy of Sciences, Washington, D.C. 237pp.

NAS. 1984. Leucaena: Promising Forage and Tree Crop for the Tropics. Innovations in Tropical Reforestation; Second Edition, National Academy Press, Washington, D.C. 100pp.

Napompeth, B. 1995. Leucaena psyllid in the Asia Pacific region: Implications for its management in Africa. *In* Ciesla, W.M. and L. Nshubemuki, (eds.), Leucaena Psyllid: a threat to agroforestry in Africa. Proceedings of a Workshop, 10-24 October, Dar-es-Salaam, United Republic of Tanzania. FAO, pp. 114-135.

Napompeth, B. and K.G. MacDicken (eds.). 1990. Leucaena psyllid: Problems and Management. Winrock International/IDRC/NFTA/F-FRED. Bangkok, Thailand, 208pp.

Ndayiragije, P. and K. Salvator. 1995. Leucaena Psyllid in Burundi. *In* Ciesla, W..M. and L. Nshubemuki, (eds.), Leucaena Psyllid: a threat to agroforestry in Africa. Proceedings of a Workshop, 10-24 October, Dar-es-Salaam, United Republic of Tanzania. FAO, p 57.

NFTA (Nitrogen Fixing Tree Association). 1987. Proceedings of a workshop on the biological and genetic control strategies for the leucaena psyllid. D. Worthington and J.L. Brewbaker, (eds.), Leucaena Research Reports (Special issue) 7(2), Waimanolo, Hawaii, 109pp.

Ngambeki, D.S. 1985. Economic evaluation of alley cropping leucaena with maize-maize and maize-cowpea in southern Nigeria. Agric Systems 17: 243 - 358.

Nye, I. W. B. 1960. The insect pests of graminaceous crops in East Africa. Col. Res. Studies No. 31, H.M.S.O.,London, 48pp.

Odhiambo, T.R. 1990. Assets for an IPM specialist with particular reference to *Chilo*. Insect Sci. Application Vol 11, No. 4/5, pp. 571-576.

Okigbo, B.N. and D.J. Greenland. 1977. Intercropping systems in tropical Africa. *In* Multiple Cropping. American Society of Agronomy, Special Publication No. 27 pp.63-101.

Otsyina, R. and B. Dwodzela. 1995. Importance of Leucaena in Africa. *In* Ciesla, W.M. and L. Nshubemuki, (eds.), Leucaena Psyllid: a threat to agroforestry in Africa. Proceedings of a Workshop, 10-24, October, Dar-es-Salaam, United Republic of Tanzania. FAO, pp. 25-39.

Overholt, W. A., K. Ogedah and P. M. Lammers. 1994. Distribution and sampling of *Chilo partellus* (Lepidoptera: Pyralidae) in maize and sorghum on the Kenya coast. Bull. Ent. Res. 84: 367-378.

Papendick, R. I., P. A. Sanchez and G. B. Triplett (eds.), Multiple cropping, ASA (American Society of Agronomy) Spec. Pub. 27, Madison, WI.

Päts, P. 1992. Reproductive biology of the cereal stem borer Chilo partellus. Ph.D. dissertation, Swedish University of Agricultural Sciences, Uppsala, Sweden. 97pp.

Päts, P. & S. Wiktelius. 1992. Diel flight periodicity in *Chilo partellus*. Entomol. exp. appl. 65: 165-170.

Perrin, R. M. 1977. Pest management in multiple cropping systems. Agroecosystems 3, 93-118.

Perrin, R. M. and R. M. Phillips. 1978. Some effects of mixed cropping on the population dynamics of insects. Entomol. Exp. Appl. 24: 385-393.

Pimentel, D. 1961. Species diversity and insect population outbreaks. Ann. Ent. Soc. Am. 54: 76-87.

Pound, B and L. Martinez Cairo. 1983. Leucaena: Its cultivation and use. London, Overseas Development Administration.

Prasad, R. 1978. Management practices for improving maize yield .*In* J.C. Holmes (ed.), Technology for increasing food production. FAO, Rome. 554-558.

Price, P. W. and G. P. Waldbauer. 1975. Ecological aspects of pest management. *In* R. L. Metcalf and W. H. Luckman, (eds.), Introduction to insect pest management. John Wiley and Sons, New York, pp. 37-73.

Proverbs, G. 1985. Leucaena, a versatile plant. Caribbean Agric. Res. Dev. Inst., Barbados, West Indies.

Rao, M.R. 1995. Leucaena psyllid in Kenya and experience with chemical control. *In* Ciesla, W.M. and L. Nshubemuki, (eds.), Leucaena Psyllid: a threat to agroforestry in Africa. Proceedings of a Workshop, 10-24 October, Dar-es-Salaam, United Republic of Tanzania. FAO, pp. 136-142.

Rawanawshah T. 1995. The leucaena psyllid in Mauritius. *In* Ciesla, W. M. and L. Nshubemuki, (eds.), Leucaena Psyllid: a threat to agroforestry in Africa. Proceedings of a Workshop, 10-24 October, Dar-es-Salaam, United Republic of Tanzania. FAO, pp.78-80.

Reynolds, L. and S. Bimbuzi. 1992. Leucaena psyllid arrives in Kenya. Agroforestry today, 4(3): 2.

Risch, S. J., D. Andow, and M. A. Altieri. 1983. Agroecosystem diversity and pest control: Data, tentative conclusions, and new research directions. Environ. Entomol. 12: 625-629.

Root, R. B. 1973. Organization of plant - arthropod association in simple and diverse habitats: The fauna of collards (*Brassicae olevaceae*). Ecol . Monogr. 43: 95-124.

Rundquist, F. M. 1984. Hybrid Maize Diffusion in Kenya. Policies, diffusion patterns and consequences. Case studies from Central and South Nyanza Provinces. CWK Gleerup, Lund.

Shakacite, O. 1995. Distribution of leucaena, current status and impact of leucaena psyllid and some management options for Zambia. *In* Ciesla, W.M. and L. Nshubemuki, (eds.), Leucaena Psyllid: a threat to agroforestry in Africa. Proceedings of a Workshop, 10-24 October, Dar-es-Salaam, United Republic of Tanzania. FAO, pp. 107-111.

Sheshu Reddy, K.V. 1983. Studies on the stem-borer complex of sorghum in Kenya. Insect Sci. Application Vol. 4, No. 1/2. pp3-10.

Sheshu Reddy, K.V. 1991. Insect pests of sorghum in Africa. Insect Sci Application 12, 563-657.

Skoroszewski, R. W. & H. Van Hamburg. 1987. The release of *Apanteles flavipes* (Cameron) (Hymenoptera: Braconidae) against stalk-borers of maize and grain-sorghum in South Africa. J. ent. Soc. sth.Afr. 50, 249-255.

Southwood, T. R. E. and M. J. Way. 1970. Ecological background to pest management. *In* R. L. Rabb and F. E. Guthrie, (eds.), Concepts of pest management, North Carolina State University, Raleigh, pp. 6-28.

Sumberg, J.E. and C. Okali. 1983. Linking crop and animal production. A pilot development program for rural small holders in southwest Nigeria. Rural Development in Nigeria 1.

Swaminathan, M. S. 1987. The promise of agroforestry for ecological and nutritional security. *In* H. A. Steppler and P. K. R. Nair. (eds.), Agroforestry: a decade of development. International Council for Research in Agroforestry, Nairobi, Kenya. pp. 25-41.

Tahvanianen, J. O. and R. B. Root. 1972. The influence of vegetational diversity on the population ecology of specialized herbivore, *Phyllotreta crucifera* (Coleoptera: Chrysomelidae) . Oecologia 10: 321-346.

Vandermeer, J. H. 1990. Intercropping. *In* C. R. Carrol, J.H. Vandermeer and P. M. Rosset (eds.), Agroecology. McGraw Hill, New York. pp. 481-516.

van Emden, H. F and G. C. Williams. 1974. Insect stability and diversity in agroecosystems. Annu. Rev. Entomol. 19: 455-475.

van Hamburg, H. 1979. The grain-sorghum stalk borer *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae): seasonal changes in adult populations in grain sorghum in the Transvaal. J. ent. Soc. sth.Afr. 42(1), 1-9.

Vietmeyer, N. D. 1979. Tropical tree legumes: a front-line against deforestation. Ceres (71) 12, No. 5, pp. 38-41.

Waage, J. 1990. Exploration for biological control agents of Leucaena psyllid in tropical America. *In* B. Napompeth and K.G. MackDicken, (eds.), Leucaena psyllid: Problems and Management. Winrock International/IDRC/NFTA/F-FRED. Bangkok, Thailand, pp.144-152.

Webster, C. C. and P. N. Wilson. 1966. Agriculture in the tropics. Longmans, London.

Wilhelm, S. 1976. The agroecosystem: a simplified plant community. *In* J. L. Apple and R. F. Smith, (eds.), Integrated Pest Management. Plenum, New York, pp 59-70.

2. MAIZE STEM BORER COLONIZATION, ESTABLISHMENT AND CROP DAMAGE LEVELS IN THE MAIZE-LEUCAENA AGROFORESTRY SYSTEM

2.1 INTRODUCTION

Small scale farmers in the tropics have long used crop diversity to minimize the risk of crop failure, improve nutrition and produce high yields of particular crops (Litsinger and Moody, 1976). Vegetational diversity within agricultural fields can be attained in many ways including intercropping, cover cropping, weedy culture (Andow, 1991) and agroforestry. Such approaches to increasing vegetational diversity in agricultural settings has been acclaimed to provide some measure of protection from insect pest attack when compared to monocultures (Altieri & Letourneau, 1982; Altieri et al., 1977; Andow, 1983a, b, 1986, 1988; Risch 1980, 1981; Risch et al., 1983; Gold et al., 1990; Midmore & Alcazar, 1991). Consequently, vegetational or crop diversity has been frequently recommended as a way of reducing pest problems, and lack of it has been blamed for some problems in agriculture (Tonhasca and Byrne, 1994). On the other hand, several reports indicate that diversity either had no effect or caused increases in density of insect pests (Andow, 1986, 1988; Cromartie, 1975; Kareiva, 1987). Hence, recommendations based on a general hypothesis of pest suppression are questionable since specific outcomes may be influenced by complex ecological interactions within particular systems.

Several studies and theoretical arguments suggest that differences in pest abundance between diverse and simple systems can be accounted for by the response of herbivore host finding bahaviour to patterns of resource availability (Risch et al., 1983). This phenomenon is known as the "resource concentration hypothesis" (Root, 1973, 1990). This hypothesis, which largely applies to specialist herbivores, suggests that non-host species disrupt the ability of a pest to attack its proper host efficiently. Andow (1983a) stated that the relative "attractiveness" of a habitat for a particular pest insect

determines the "resource concentration" of that habitat and can be affected by the following interacting factors: (1) the number of host plant species present and the relative preference of the insects for each, (2) the absolute density and spatial arrangement of each host species, and (3) interference from non-host plants. At lower relative resource concentrations, the pest may have more difficulty locating a host plant, a greater propensity to leave it, or a lower reproductive rate on it.

The aim of my study was to examine the role of resource concentration on insect pest populations in a particular agroforestry system involving maize and the tree legume *Leucaena leucocephala*. Studies in Kenya and Nigeria have reported higher yields of maize when alley cropped with leucaena (Macklin et al., 1989; Kang et al., 1984). Furthermore, it has been demonstrated that maize yields can be kept constantly high when continuously intercropped with leucaena prunings alone (Kang et al., 1984). This production technology can have significant positive impact on maize yields particularly among the large population of resource-limited subsistent farmers of East Africa for whom maize is a staple food crop. My study involved alley cropping leucaena with maize under varying spatial arrangements and/or cultural management and establishing whether these practices had any effect on the host finding, colonizing ability and abundance of stem boring lepidopterans, the principal pests of maize in East Africa. I also studied the resultant effect on damage levels and yield losses caused by these pests. Under the resource concentration hypothesis, the maize intercrop would be expected to provide some level of protection by the leucaena from insect pest attack. This could contribute to the development of new, environmentally safe, cost effective and sustainable pest management methods for tropical Africa. This would be particularly useful for stem borers of maize whose pervasiveness in the field throughout the growing season makes effective control difficult and costly.

2.3 MATERIALS AND METHODS

2.3.1 Study sites

These studies were conducted mainly at the Kenya Agricultural Research Institute (KARI) Regional Research Centre at Mtwapa, Coast Province, Kenya (3°56' S, 39°44' E and 15m above sea level). At the coast, soils are generally sandy and deficient in nutrients, especially nitrogen and phosphorous (Warui and Kuria, 1983). Average rainfall is about 1200mm per year, which tends to decrease towards the north and interior. Rainfall is bimodal, allowing the cultivation of two crops annually. Temperatures are generally high (25 - 30° C) throughout the year (Warui and Kuria, 1983). Agriculture in the coastal strip is characterized by predominantly tree-based systems in which trees such as coconut palms, cashews and mangoes are intercropped with cassava and/or maize with or without livestock grazing. Alley cropping may be a useful alternative farming system (Macklin et al., 1989), especially given historical evidence of high populations of maize stem borers (Mathez, 1972; Scheltez, 1978; Warui and Kuria, 1983).

Supplementary studies were carried at Kenya Forestry Research Institute experimental field site at Amoyo, Nyanza Province (0°10' S, 34°23 E and approximately 1400m above sea level (Figure 2.1). Documented, site-specific data for Amoyo are lacking. Nevertheless, from personal observations, it has a bimodal rainfall pattern allowing the cultivation of two crops annually. The onset of both rainy seasons is unpredictable and rainfall distribution is highly variable, sometimes excessive during the long rains and, inadequate (or too short) during the short rains. The area is classified as moisture availability zone IV and described as semi-arid to semi-humid type (Sombroek et al., 1982), and lack of sufficient moisture results in frequent crop failures. The vegetation is typical savanna type with grassland and variably spaced trees (mostly *Acacia*). The soils are variable but mainly clay in texture and in certain areas, poorly drained and often difficult to till. Livestock husbandry (cattle, goats and a few sheep and donkeys) and intercropping of annuals (maize, sorghum, finger millet, cowpeas and peanuts) and perennials (cassava) are the most important agricultural activities. Trees are greatly

threatened in the region because of the ever increasing fuel needs of the more populous surrounding. Consequently, the Kenya Forestry Research Institute (KEFRI) has been promoting agroforestry among the local community in hopes of ameliorating impacts of deforestation and improving food and fibre production.

2.3.2 Experimental Design and Plot-layout.

Five month old seedlings of *Leucaena leucocephala* (Lam) de Wit were planted in hedgerows at Mtwapa and Amoyo during the short rains of 1992. Plots at Mtwapa measured 18 x 12m and those at Amoyo were 12 x 10m. Plots were separated by 6m buffer strips of bare ground. Trees within hedgerows were spaced at 0.5 m. At Mtwapa, six plots were randomly assigned between row spacings of 1.5m, 1.5m, 2.25m, 2.25m, 2.25m and 3.0m and, at Amoyo, five plots were assigned spacings of 1.5m, 2.25m, 2.25m, 2.25, and 3.0m. At both sites, an additional plot was planted to maize alone. This served as a control for the evaluation of the intercrop effect. Plots were laid out in a randomized complete block design, and with five replicates at Mtwapa (35 plots total, Figure 2.2) and four replicates at Amoyo (24 plots total, Figure 2.3).

During the cropping seasons associated with the short rains of 1992, long and short rainy seasons of 1993 and 1994 and the long rains of 1995, maize was planted between the hedgerows of leucaena except for one of the 1.5m plots at Mtwapa, which served as a control for the evaluation of the hedgerow effect. Maize was planted at a spacing of 30cm within rows, 75cm between rows and 75cm between rows of maize and the leucaena hedgerows. Thus, 1, 2 and 3 rows of maize were planted between hedgerows planted 1.5m, 2.25m and 3m apart respectively (Table 2.1). The locally recommended Hybrid 512 maize variety was planted at Amoyo while Pwani Hybrid was planted at Mtwapa. A day after planting of maize, the leucaena were cut back to 30cm above ground. The twigs and leaves were weighed first and then applied as mulch except for one set of plots with 2.25m spacing. Plots were hand weeded twice during the cropping season except for another of the 2.25m spaced plots.

2.3.3 Data collection

Due to the extensive and labourious nature of the studies, sampling and general data collection was performed with the assistance of locally recruited and trained field assistants. As many as 7 assistants were involved depending on the task at hand.

The studies have been grouped into three main sections based on the mechanisms and effects of the resource concentration hypothesis. The first (2.3.4) deals with host seeking behaviour, the second (2.3.5), stem borer population development, survival and aspects of the damage that these insects cause and, the third (2.3.6), yield assessment. All studies were conducted at Mtwapa while only the first two of the three under the section on larval activity and plant damage (2.3.5.1 & 2.3.5.2) were conducted at Mtwapa and Amoyo.

2.3.4 Adult activity and Oviposition

2.3.4.1 Abundance and distribution of adult *Chilo* spp.

The stem borers encountered at Mtwapa consisted of three species; *Sesamia calamistis*, *Chilo partellus* and *Chilo orichalcociliellus*. Estimates of adult abundance were possible for *Chilo* spp only using a synthetic pheromone that could be used to capture males.

To obtain an estimate of adult abundance of *Chilo* spp at Mtwapa, the methodology of Lux et al.(1994) was used. Synthetic female *C. partellus* pheromone components (Z)-11-hexadecenal (Z11-16:Ald) and (Z)-11-hexadecenal-1-ol (Z11-16:OH) were obtained from commercial sources with their purity confirmed to be greater than 99% by GC analysis. This pheromone attracts both *Chilo partellus* and *Chilo orichalcociliellus* (Lux, unpublished). One square filter paper ($2.5cm^2$) was loaded with 100µl n-hexane solution containing 100 µg of the aldehyde component and the other

paper with 100 µl hexane containing 10 µg of the alcohol component. For close release, loaded filter papers were separated by a piece of polyethylene foil and held together with a foil covered paper clip. Dispensers were mounted on Phercon I C traps which were placed 50 cm from the ground, one at the center of each plot. Adult moths were collected and counted twice weekly (Wednesday and Sunday) for a period of one year (Dec. 1993 - Nov. 1994). Fresh pheromone was loaded onto the traps during each moth collection day. Both species of *Chilo* were expected to respond equally to the sex pheromone (Lux pers. comm.), so data were pooled for analysis.

2.3.4.2 Oviposition preference

From 8 days after plant emergence, the foliage of all maize plants was carefully inspected for stem borer egg batches. These were counted and data were expressed as number of stem borer egg batches per plot and per plant. This was repeated weekly for three weeks during the first three cropping seasons. However, during the last three cropping seasons, sampling was biweekly for 8 weeks.

2.3.5 Larval activity and plant damage

2.3.5.1 Foliar damage

At 4 weeks after emergence of maize seedlings (WAE), the foliage of all maize plants were inspected for stem borer damage. All plants were counted including the total number of maize plants per plot. Data were expressed as percentage of plants with foliar damage per plot.

2.3.5.2 Stem borer activity and prevalence

From 8 WAE, ten maize plants were randomly sampled from each plot. Stalks were inspected for stem borer entry or exit holes. Counts were recorded and expressed as number of entry or exit holes per 10 plants and the percentage of plants with entry/exit holes. This was repeated every three weeks and at harvest. The stalks were then split open to assess stem borer prevalence. The number of larvae, pupae and pupal cases were counted for each stem borer species. Larvae and pupae obtained were maintained for other studies. Data obtained was expressed as number of borers per 10 plants and percentage of plants with borers.

2.3.5.3 Prevalence of dead plants and stem breakage

At peak flowering/tasselling stage, the total number of maize plants dead from the effect of severe stem-borer infestation were counted in each plot. Such plants characteristically showed symptoms of severe foliar and stem damage, deformation and retarded growth. Data obtained was expressed as percentage plants dead per plot. Plants with broken stalks were counted and expressed as percentage of plants with broken stalks per plot.

2.3.6 Yield assessment

During harvest at Mtwapa, 20 maize plants were randomly selected and the number of ears counted and expressed as number of ears per 20 plants and percentage of plants with ears. This was increased to 40 plants per plot during the short and long rains of 1994. Ears from the selected plants were collected, stored separately according to plot, sun dried and weighed individually. These were then shelled individually and the seeds weighed. These data were expressed as average weight of seed per plant for plants with ears. Yield per plot was calculated by subtracting the additive effect of loss from plant

mortality, stem breakage and plants without ears from the potential maximum number of plants per plot from number of holes seeded [(potential maximum maize plants per column) (number of rows of maize per plot)] and multiplying this number by the average weight of seeds per plant for each plot. This data was expressed as weight of seeds per plot. The latter value was then divided by the potential maximum number of plants per plot to obtain yield per plant that took into consideration all potential plants per plot. Thus, yield was assessed in three ways; (1) weight of seeds per plant for only those plants with ears, (2) weight of seeds per plot, and (3) weight of seeds per plant for potential number of plants per plot.

2.3.7 Data Analysis

Data collected were averaged for individual plots during each cropping season because of the unequal frequency of samples taken during the seasons, and analyzed by two-way (treatment x seasons) analysis of variance (ANOVA) (PROC GLM, SAS Institute, 1985) both on actual and arcsine transformed data. However, data for abundance of *Chilo* spp adults were pooled per plot for the entire trapping period and analyzed by one-way ANOVA. Thereafter, pre-planned orthogonal comparisons were made to test respectively, for effects of intercropping, weeds and mulch. In addition, regression analysis (PROC REG, SAS Institute, 1985) was used to test for linear and quadratic relationships of spacing to the infestation and damage variables. A summary of post-ANOVA data analysis is shown in Table 2.2. Although two-way ANOVA was used in the analysis of data, only the effect of treatments have been included in the results herein.

2.4 RESULTS

2.4.1 Adult activity and Oviposition

2.4.1.1 Adult *Chilo* spp. abundance and distribution.

The highest number of *C. partellus* and *C. orichalcociliellus* moths were captured in the maize monocrop plot (Figure 2.4) and the *a priori* tests indicate that the captures were significantly higher in the maize monocrop than in the intercropped plots (Table 2.3). The *a priori* comparisons also suggest that there were no significant differences between the unweeded plots and the weeded plots and between the unmulched plots and mulched plots. Significantly fewer moths were captured in the leucaena monocrop plot as compared to plots with maize. Spacing did not show significant linear or quadratic relationship with adult captures (Table 2.3) suggesting that spacing had no effect on the population of moths. Thus, intercropping with leucaena significantly reduced the number of males responding to the pheromone signals.

2.4.1.2 Oviposition preference

The maize monocrop had the greatest number of stem borer egg batches (Figure 2.5a) and the *a priori* comparisons suggest that the eggs were significantly more abundant in the maize monocrop than in the intercrops (Table 2.4a). Similarly, the comparisons suggest that there were significantly fewer eggs in the unweeded plot than in the weeded plots and in the unmulched than in the mulched plot. However, there was no significant linear or quadratic relationship between maize spacing and the number of eggs laid (Table 2.4a). Thus, intercropping, weeds and mulch significantly reduced the number of stem borer eggs oviposited per plot while spacing had no effect.

The overall ANOVA of data expressed as percentage of plants with egg batches (Figure 2.5b) revealed significant differences among treatments. However, the *a priori*

tests show that the proportions did not differ significantly between the maize monocrop and the intercrops (Table 2.4b). Similarly, the contrasts show no significant differences between the unweeded plot and the weeded plots and between the unmulched and mulched plot. There was however a significant inverse linear relationship between spacing and the proportion of plants with eggs, suggesting that the proportion of plants with eggs decreased with increased hedgerow spacing.

2.4.2 Larval activity and plant damage

2.4.2.1 Foliar Damage

The percentage of plants with foliar damage were highest in the maize monocrop plot at Mtwapa (Figure 2.6a) and clearly, the damage was significantly higher in the maize monocrop than in the intercropped plots (Table 2.5). On the other hand, the contrasts suggest that there were no significant differences between the unweeded plots and the weeded plots nor between the unmulched and mulched plots. Similarly, there was no significant linear or quadratic relationship between spacing and the percentage of plants with foliar damage. Thus, intercropping significantly reduced the proportion of maize plants with foliar damage at Mtwapa. However, at Amoyo, there were no significant ($F = 0.045$, $df = 5,90$, $P = 0.81$) differences between treatments (Figure 2.6b), and the contrasts show that vegetation structure had no consistent effect on foliar damage (Table 2.5).

2.4.2.2 Stem borer prevalence

Stem borers encountered at Mtwapa were *Sesamia calamistis* (Lepidoptera: Noctuidae), *Chilo partellus* (Lepidoptera: Pyralidae) and *Chilo orichalcociliellus* (Lepidoptera: Pyralidae), while *Sesamia calamistis*, *Chilo partellus* and *Heliothis armigera* (Lepidoptera: Noctuidae) occurred at Amoyo. At both sites, the maize

monocrop had the greatest mean number of borers per 10 plants (Figures 2.7a & b respectively). However, given the high variances observed, the linear contrasts showed no significant differences among treatments (Table 2.6).

When data was analyzed as percentage of plants with borers, the maize monocrop again had the greatest proportion of plants with borers at both sites (Figures 2.8a & b respectively), and the *a priori* comparisons establish that the proportions were significantly greater in the maize monocrop plot than in the intercropped plots (Table 2.7). However, the pre-planned contrasts show no significant differences between the unweeded and the weeded plots nor between the unmulched and the mulched plots. Similarly, there was no significant linear or quadratic relationship between spacing and the percentage of plants with borers. Thus, intercropping generally reduced the proportion of maize plants with borers at both sites, but different intercrop treatments had little effect.

2.4.2.3 Stem borer entry/exit holes

At both Mtwapa and Amoyo, the maize monocrop had the greatest number of stem-borer entry and exit holes per 10 plants (Figures 2.9a & b respectively) and the *a priori* comparisons show that damage was significantly higher in the maize monocrop than in the intercropped plots (Table 2.8). Thus, intercropping significantly reduced the number of entry or exit holes at both sites. On the other hand, the *a priori* comparisons suggest that there were no significant differences between the unweeded plot and the weeded plots and between the unmulched and mulched plots. Similarly, there was no significant linear or quadratic relationship between spacing and the number of entry or exit holes at Mtwapa. At Amoyo, there was no significant linear relationship with spacing. However, a significant quadratic response suggests that the median spacing (2.25m) was the optimal spacing below or above which there will be a significant increase in the number of entry and exit holes.

When data were analyzed as percentage of plants with entry and exit holes, a greater percentage of plants had damage holes in the maize monocrop plot at Mtwapa (Figure 2.10a) and the pre-planned comparisons indicate that significantly more holes were found in the maize monocrop than in the intercropped plots (Table 2.9). However, the comparisons reveal no significant differences between the unweeded and the weeded plots nor between the unmulched and mulched plots. Similarly, there was no significant linear or quadratic relationship between spacing and the percentage of plants with foliar damage. Thus, intercropping significantly reduced the proportion of maize plants with entry or exit holes at Mtwapa. At Amoyo however, there were no significant ($F = 0.20$, $df = 5,90$, $P = 0.96$) differences among treatments (Figure 2.10b) and the *a priori* comparisons show that vegetation structure had no effect on the proportion of maize plants with entry and exit holes (Table 2.9).

2.4.2.4 Plant mortality

More plants died in the maize monocrop (Figure 2.11) and the *a priori* comparisons indicate that this difference was significant between the maize monocrop and the intercropped plots (Table 2.10). On the other hand, the contrasts show no significant differences between the unweeded and the weeded plots nor between the unmulched and mulched plots. Similarly, there was no significant linear or quadratic relationship between spacing and plant mortality.

2.4.2.5 Stem breakage

The maize monocrop had the greatest average percentage of plants with broken stems (Figure 2.12). However, the linear contrasts showed no significant differences among treatments (Table 2.11), suggesting that the treatments had no effect on the proportion of stems broken.

2.4.8 Yield of maize

Yield was first calculated for sampled plants with ears. Data obtained was expressed as average weight of seeds per plant for plants with ears (Figure 2.13a). The pre-planned contrasts established that the maize monocrop and the intercrops did not differ significantly (Table 2.12a). However, the contrasts suggest that seed weight from the weeded plots were significantly higher than those from unweeded plots. Also, seed weight from the mulched plots were significantly higher than those from unmulched plots. There was, however, no significant linear or quadratic relationship between spacing and seed weight.

Yield was then computed for all potential plants per plot. This data which was expressed as weight of seeds per plant for all plants show that three of the intercrops (1.5m, 2.25m and 3.0m) had greater yield than the maize monocrop (Figure 2.13b). *The a priori* comparisons suggest that collectively, there were no differences in yield between the intercrops and the monocrop (Table 2.12b). However, when the intercrops were partitioned with respect to cultural treatments (weeding and mulching), the contrasts indicate a highly significant reduction in yield in the maize monocrop plot compared to the three intercropped plots (mentioned above) that were both weeded and mulched. However, yield of the monocrop plots cannot be distinguished from that of the unmulched intercropped plots, and was significantly greater compared to the unweeded plots. There was no significant linear or quadratic relationship between spacing and seed weight per plant. Thus intercropping significantly increased yield over monocropping, but only when plots were weeded and mulched.

Finally, yield was calculated per plot, and the 3.0m intercrop plot had the highest mean maize yield (Figure 2.13c). However, the *a priori* comparisons indicate that this yield was not significantly higher than in the maize monocrop plot. Nevertheless, it was significantly superior to all the other intercropped plots (Table 2.12c). The linear contrasts also show that there were significant differences between the maize monocrop and the intercropped plots with the former tending towards the higher side (except for

comparisons with the 3.0m plots). Similarly, there were significantly higher yields from the weeded plots than the unweeded plots and in the mulched plots than the mulched plots. There was significant positive linear relationship between spacing and yield per plot suggesting that yield increased with increasing hedgerow spacing. Thus, intercropping at 3.0m gave the same per plot yield as the maize monocrop, or even tended to be higher than the monocrop, despite having 25% lower maize plant density than the latter.

2.5 DISCUSSION AND CONCLUSIONS

2.5.1 Maize stem borer-host seeking and colonization ability.

Colonization by maize stem borers was significantly reduced in the maize-leucaena intercrops as compared to the maize monocrop. This was clearly reflected, both in the population densities of colonizing *Chilo* spp. adults captured in pheromone traps, and in the data about oviposition. These results are consistent with reports for other plant-herbivore systems in which there were fewer colonizing adults in polycultures than in monocultures (Bach, 1980a, b; Coll and Bottrel, 1994; Risch, 1981), and with those in which intercropped maize consistently received fewer egg masses than monocropped maize (IRRI, 1974; Suryatna, 1976; Coll and Bottrell, 1994).

My results are concordant with aspects of the resource concentration hypothesis which predict greater herbivore numbers in simple than in diverse habitats. *Chilo* spp. are more-or-less specialist herbivores on maize (and other grasses) and apparently, are less likely to locate their host plant efficiently in diverse habitats because of the masking and dilution of the attractant stimuli by non-host plants such as leucaena. The greater number of adults captured in the maize monoculture than in the intercrops may have resulted primarily from the greater ease of pheromone source detection and location in the former. However, there was an apparent interaction between the host-plant chemical factor and the pheromone resulting in the significantly lower incidence of adult *Chilo* spp in the non-host leucaena monoculture when compared to other treatments which had maize. Thus,

perhaps a host plant factor is necessary for greater attractancy to the sex pheromone. There is, however, no evidence that male moths are attracted by volatiles of juvenile-stage host plants without the simultaneous presence of sex pheromones.

Host location was also probably affected by the presence of both leucaena and weeds which, reduced the borers ability to physically locate their host efficiently as shown by the lower egg batches in the intercropped and weeded plots. Thus, a second component of the resource concentration hypothesis that non-hosts act as mechanical barriers by blocking the dispersal of herbivores across the polyculture, may also apply. This was further supported by the field observation that *Chilo* spp. egg batches were often deposited on weeds, suggesting that the herbivore's mobility during the host-seeking process may have been physically strained or obstructed by weeds.

My studies suggest that the spacing of leucaena hedgerows had no significant influence on the stem borer's response to the pheromone and oviposition preference. These results are consistent with those of Bach (1980) who emphasized the importance of plant diversity *per se*, rather than density, in influencing pest populations. This provides flexibility for the agroforester to choose the spatial regime that best serves needs for local conditions while still maintaining optimal reduction of colonizing stem borers.

In conclusion, a number of resource concentration mechanisms among those enumerated by Altieri and Liebman (1986), may be hypothesized as being responsible for my observations: (1) that non-host plants chemically mask the moth's olfactory attractiveness to the sex pheromone and the host plant; (2) that non-host plants act as physical barriers for the moth's movement toward sex attractant and the host plant; (3) that there is an association between host plant chemical stimuli and the sex attractant; and (4) a combination of two or more of the factors mentioned above. Studies aimed at elucidating these mechanisms are necessary to further understand the basis of resource concentration in pest populations dynamics in this particular agroforestry system.

2.5.2 Stem borer abundance and damage levels

Pest abundance and damage parameters that were significantly reduced in intercrops compared to the maize monocrop include foliar damage, percentage of plants with borers, number of stem borer entry and exit holes, percentage of plants with entry and exit holes and plant mortality. All the above were observed at Mtwapa while at Amoyo, neither measures of foliar damage nor percentage of plants with entry or exit holes differed among treatments. Percentage of plants with broken stems at Mtwapa and number of borers per plant at either site, did not differ significantly between the monoculture and intercrops.

My results are consistent with several results of other related studies. Ampong-Nyarko et al. (1994) and Dissemond and Hindorf (1990) reported a reduction in the percentage of stem borer foliar damage in sorghum/cowpea intercrop when compared to a sorghum monocrop. Ampong-Nyarko et al. (1994) further reported both significant and non-significant reduction in numbers of *Chilo partellus* larval and pupal densities in the intercrop as compared to monocrops of sorghum. Martin et al. (1989) reported significantly lower percentage infestation by European corn borer (*Ostrinia nubilalis*) in intercropped (corn/soybean) than in monocropped tall corn. Similarly, in a cassava/maize system, Gold et al. (1990) recorded fewer stem borer holes in the intercrops than in the monocrop of cassava by the cassava stem borer, *Chilomima clarkei* (Lepidoptera: Pyralidae).

Incidence and proportion of foliar damage, borer abundance and proportion of plants infested can be attributed to both ovipositional and larval distribution patterns. The former will directly influence which plants will be infested and damaged upon hatching of eggs. The latter is achieved through movement of larvae, particularly small larvae. This is inevitable because *Chilo* eggs are laid in batches containing a few to more than a hundred eggs (Päts and Ekbom, 1994), yet a single maize plant can support only up to 24 larvae to full term (Berger, 1992). This means that larvae hatching from an egg batch on a particular

maize plant will not be able to develop to full term on that plant. Consequently, small larvae have to disperse to adjacent plants by "spinning or ballooning off" (Chapman et al., 1983; Ampofo, 1986; Berger, 1989; Päts and Ekbom, 1992). During this dispersal, young larvae may die if they fail to locate a new and suitable host plant, are taken by natural enemies or are exposed to adverse weather conditions (Päts and Ekbom, 1992).

Leucaena plants may act as mechanical barriers, restricting the dispersal of young larvae in intercrops, leading to mortality by starvation, or exposure to adverse weather conditions and/or possible depredation by natural enemies (see Chapter 3). Because the percentage of plants with stem borer eggs did not differ significantly among treatments (Figure 2.6), the significant differences in infestation and damage rates observed between the monocrop and intercrops must reflect mainly differences among the treatments with respect to ease of host location during larval dispersal. I conclude that non-hosts act as mechanical barriers, blocking the dispersal of herbivores across the polyculture.

Maize plant mortality was a consequence of severe stem borer damage during the early stages of plant growth, particularly when soil moisture was limiting, as occurred most conspicuously during the short rains. The greater percentage of dead plants observed in the maize monocrop than in the maize-leucaena intercrops clearly suggest greater devastation by stem borers, similarly influenced by the component of the resource concentration hypothesis mentioned above. Despite paucity of comparative data on the effect of stem borers on host plant mortality in the literature, percentage plant mortality appears to be a good measure of the effect of stem borer damage on cereals. It appears that this measure could be a fundamental component of yield loss assessment of maize from stem borer attack, particularly well suited to the East African situation.

In all cases where there were significant differences between treatments, there were no significant effects of weeds, mulch and spacing, suggesting the strong and singular influence of leucaena as an intercrop in reducing and maintaining pest populations in agroecosystems. Moreover, since the maize monocrop consistently exhibited greatest damage in all variables where there were no significant differences among treatments,

weakly suggests that the intercrop situation may have protected the maize from damage by stalk borers.

2.5.3 Effect of stem borers on yields

There was no difference between the monocrop and intercrops in seed yield per plant for plants with cobs. However, in the intercrop situation, weeds and lack of mulch caused significant reduction in this measure of yield. This method of yield assessment ignored other damage parameters and thus does not reflect the 'true' and total crop loss. Nonetheless, it is useful for calculating absolute yield once the proportion of plants lost to various other effects have been partitioned.

When yield was calculated over all plants originally seeded, the three mulched and weeded intercropped plots had significantly greater seed weight per plant than the maize monocrop. These results are consistent with other studies that have reported increased maize yields when intercropped with leucaena (Kang et al., 1989, 1990; O'Sullivan, 1985; Macklin et al., 1989). These increases have been accredited to the positive effects of leucaena prunings of soil fertility alone.

The maize monocrop and the unmulched plot obtained equal seed yield per plant. However, plant competition may have influenced these results. Studies abound which have attributed the lower yields of maize and cowpea when alley cropped with leucaena to severe competition for moisture (Lal, 1989). Furthermore, studies conducted in Peru showed that crop yields from alley cropped plots were equal to or less than that from the control monocropped plots and this was attributed to root competition and shading (Szott, 1987; Fernandes, 1990). It can therefore be argued that in the unmulched intercrop, the negative effect of plant competition tended to balance out the positive effect of protection from pests, yielding seed weight per plant equal to the monocrop which had reduced protection from pests but experienced relatively less plant competition. Therefore, it appears that to achieve effective crop protection in agroforestry that translates into yield

advantage, the cultural practices of weeding and mulching are crucial components of crop management.

The overall yield of maize per plot was highest in the 3.0m intercrop plot while all the other intercrops were outyielded by the monocrop. Furthermore, the unweeded and the unmulched plots were significantly outyielded by the weeded and mulched plots respectively. In addition, yield significantly increased with increased hedgerow spacing. Yield could have been influenced by four factors in the present system; weeds, soil nutrients, spacing of hedgerow and, damage by insect pests.

Whereas weeds were an obvious cause of low yields in the unweeded plot, reduced or lower soil nutrients was probably responsible for the lower yield in the unmulched plot compared to the mulched plot. Similarly, wider spacing (and therefore increased density of maize within plot) was associated with increased yield per plot.

The effect of insect pest numbers and damage appeared to be one of the most important influences on yield since the main parameters used in the computation of yield reflected the net effect of stem borer damage to the maize plants. Moreover, considering that the maize monocrop had a greater density of maize plants than the intercrops (25% more than the 3.0m intercrop), that there was greater competition for moisture in the intercrop, and that the weight of maize seeds per plant for plants with ears (Figure 2.19, used in computing yield per plot) were not significantly different between the maize monocrop and the intercrops, the fact that yield in the 3.0m intercrop plot was equal or superior to that in the monocrop, can only be accredited to the net effect of the protective ability of intercropping with leucaena against maize stem borers. On this basis, I argue that insect pests caused greater yield reduction in the maize monocrop than in the leucaena-maize intercrop, as is consistent with other studies which reported similar effects of *Chilo partellus* on yield in sorghum/cowpea systems (Ampong-Nyarko et al., 1994). Similar results have also been reported for pests of common beans in a bean/maize systems (Karel, 1993). However, no results of comparative studies on agroforestry systems are available in the literature.

2.5.4 Conclusions

These studies show that alley cropping leucaena with maize reduced insect pest infestation, abundance and damage on the maize crop by stem borers. Furthermore, the reduced pest numbers translated into increased yield. The resource concentration hypothesis largely accounts for the reduced pest numbers and appears to be the most important phenomenon in pest reduction in this production system. Before polycultures can be used effectively as a tactic within the integrated pest management system, it is necessary to understand their effects on pest population density and crop yield loss (Andow, 1991). In my studies, there were yield advantages under conditions where alley cropping with leucaena reduced stem borer density in the companion maize crop. The 3.0m hedgerow spacing reduced stem borer density and yielded more maize than in the monocrop and other intercrops. I recommend its use for optimal crop protection and production of food and fiber in Kenya.

The benefits of resource concentration in reducing pest populations and damage may not be obvious and strong in some situations mainly due to low pest populations. This was demonstrated at Amoyo where some of the differences among treatments for the variables studied, were not significantly different because of the low pest populations. However, effects were strong and significant at Mtwapa where pest populations where often high. Nevertheless polycultural practices, particularly agroforestry, would still be recommended for a site like Amoyo considering the other benefits of such production systems. For example, the judicious use of leguminous trees in agroforestry systems can aid recycling of plant nutrients and water from the deeper soil profiles, fix nitrogen from the air, intercept fog drip, reduce soil-water evaporation, lower surface temperature, produce woodfuel, produce building materials, provide cash income, and generally increase off-season production, thus achieving more effective and efficient use of land (Douglas, 1972; Kirby, 1976; MacDaniels and Lieberman, 1979; Vietmeyer, 1979; Myers, 1980; National Academy of Sciences, 1980).

Studies conducted in West Africa have demonstrated that maize yields can be kept almost constant when continuously intercropped with leucaena prunings alone (Kang et al., 1984). However, under continuous monocrop, yields dwindle due to the irreplaceable depletion of nutrients by the crop and agents of erosion. The depletion of nutrients will ultimately lead to plants with reduced vigour and tolerance. Such plants may not be able to withstand the effect of higher pest densities associated with monocropping. Consequently, there will be an increasingly greater reduction of yields with continuous monocropping. It is on this basis that alley cropping with *Leucaena leucocephala* has great potential and could form a useful component of a sustainable, economically and technically feasible and environmentally friendly integrated pest management programme for the stem boring lepidopterous pests of maize in the tropics.

2.6 REFERENCES

Altieri, M. A. and D. K. Letourneau. 1982. Vegetation management and biological control in agroecosystems. Crop prot. 1: 405-430.

Altieri, M. A. & M. Liebman. 1986. Insect, weed, and plant disease management in multiple cropping systems, pp. 183-218. *In* C. A. Francis [ed.], Multiple cropping systems. Macmillan, London.

Altieri, M. A., C. A. Francis, A. van Scvhoonhoven and J. D. Doll. 1977. A review of insect prevalence in maize (*Zea mays* L.) and bean (*Phaseolus vulgaris* L.) polycultural systems. Field Crops Res. 1: 33-49.

Ampofo, J. K. O. 1986. Maize stalk borer (Lepidoptera: Pyralidae) damage and plant resistance. Environ. Entomol. 15: 1124-1129.

Ampong-Nyarko, K., K. V. Sheshu Reddy, R. A. Nyangor and K. N. Saxena. 1994. Reduction of insect pest attack on sorghum and cowpea by intercropping. Entomol. Exp. Appl. 70: 179-184.

Andow, D. A. 1983a. Plant diversity and insect populations in experimental agroecosystems: interactions among beans, insects and weeds. Ph.D. dissertation, Cornell University, Ithaca, N.Y. 201 pp.

Andow, D. A. 1983 b. Agricultural crop diversity and insect populations. Chapter 3. *In* D. Pimentel [ed.], Ecological aspects of pest management. Dept. Entomology, Cornell University, Ithaca, N.Y.

Andow, D. A. 1986. Plant diversification and insect population control in agroecosystems, pp. 277-386. *In.* D. Pimentel [ed.], Some aspects of integrated pest management. Dept. Entomology, Cornell University, Ithaca, N.Y.

Andow, D. A. 1988. Management of weeds for insect manipulation in agroecosystems, pp.265-301. *In* M. A. Altieri & M. Liebman, [eds.], Weed management in agroecosystems: ecological approaches. CRC, Boca Raton, Fla.

Andow, D. A. 1991. Yield loss to arthropods in diverse agroecosystems. Environ. Entomol. 10: 1228 - 1235

Bach, C. E. 1980a. Effects of plant density and diversity in the population dynamics of a specialist herbivore, the stripped cucumber beetle, *Acalymma vittata* (Fab.). Ecology 16: 1515-1530.

Bach, C. E 1980b. Effects of plant diversity and time of colonization on an herbivore - plant interaction. Oecologia 44: 319-326.

Berger, F. 1989. Ballooning activity of *Chilo partellus* larvae in relation to size of mother, egg batches, eggs and larvae and age of mother. Entomol. Exp. Appl. 50: 125-132.

Berger, F. 1992. Larval movements of *Chilo partellus* (Lepidoptera: Pyralidae) within and between plants: timing density responses and survival. Bull. Ent. Res. 73:75-83.

Chapman, R. F., S. Woodhead and E. A. Bernays. 1983. Survival and dispersal of young larvae of *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) in two cultivars of sorghum. Bull. Ent. Res. 73: 65-74.

Coll, M. and D. G. Bottrell. 1994. Effects of non-host plants on an insect herbivore in diverse habitats. Ecology 75: 723-731.

Cromartie, W. J. Jr. 1975. The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. J. Appl. Ecol. 12:517-533.

Dissemond, A. and H. Hindorf. 1990. Influence of sorghum/maize/cowpea intercropping on the insect situation at Mbita/Kenya. J. Appl. Entomol. 109: 144 - 150.

Douglas, J. S. 1972. Tree crops for forage and cash. World crops, January/February, pp. 15-19.

Fernandes, E. C. M. 1990. Alley cropping on an acid soil in the Peruvian Amazon: Mulch, fertilizer, and hedgerow root pruning effects. Ph.D. dissertation, North Carolina State University, Raleigh, NC, USA.

Gold, C. S., M. A. Altieri and A. C. Bellotti. 1990. Effects of intercropping and varietal mixtures on the cassava hornworm *Erinnyis ello* L. (Lepidoptera: Sphingidae), and the cassava stem borer, *Chilomima clarkei* (Amsel) (Lepidoptera: Pyralidae), in Colombia. Trop. Pest Manage. 36: 362-367.

International Rice Research Institute. 1974. Multiple cropping, pp. 22-24. *In* Annual Report for 1973. IRRI, Los Baños, Philippines.

Kang, B. T., G. F. Wilson and T. L. Wilson. 1984. Alley cropping: a stable alternative to shifting cultivation. IITA, Ibadan, Nigeria.

Kang, B. T., A. C. B. M. van der Kruijs and D. C. Cooper. 1989. Alley cropping for food production in the humid and subhumid tropics. *In* Kang, B. T., and Reynolds, L. (eds.), Alley Farming in the Humid and Subhumid Tropics, pp. 16-26. International Development Research Centre, Ottawa, Canada.

Kang, B. T., L. Reynolds and A. N. Atta-Krah. 1990. Alley farming. Advances in Agronomy 43: 315-359.

Kareiva, P. 1987. Habitat fragmentation and the stability of predator - prey interactions. Nature 326: 388-390.

Karel, A. K. 1993. Effects of intercropping with maize on the incidence and damage caused by pod borers of common beans. Environ. Entomol. 22: 1076-1083.

Kirby, J. M. 1976. Forest grazing: a technique for the tropics. World crops. Nov/Dec, pp. 242-251.

Lal, R. 1989. Agroforestry systems and soil surface management of tropical alfisols. Parts I-V. Agroforestry Systems 8(1): 1-6; 7-29; 8(2): 97-111; 113-132; 8(3) 197-215; 217-238; 239-242.

Litsinger, J. A., and K. Moody. 1976. Integrated pest management in multiple cropping systems, pp. 293-317. *In* R. I. Papendick, P. A. Sanchez, and G. B. Triplett [eds.], Multiple cropping. Am. Soc. Agron. Madison, Wisc.

Lux, S. A., A. Hassanali, W. Lwande and F. N. Njogu. 1994. Proximity of release points of pheromone components as a factor confusing males of the spotted stem borer, *Chilo partellus*, approaching the trap. J. Chem. Ecol. 20: 2065 - 2075.

MacDaniels, L. H. and A. S. Lieberman. 1979. Tree crops: a neglected source of food and forage for marginal lands. BioScience 29: 173-175.

Macklin, W. K., K. Reshid and B. Jama. 1989. Results of alley cropping experiments with *Leucaena leucocephala* at the Kenya Coast: an example of an appropriate soil conservation (fertility) measure. *In* D. B. Thomas, E. K. Biamah, A. M. Kilewe, L. B. Lundgren and B. O. Mochoge, (eds.), Soil conservation in Kenya. Proceedings of third national workshop, 16-19 September, 1986. Nairobi: Department of agricultural engineering, University of Nairobi and the Swedish International Development Authority, pp.272 - 280. IR - 60.

Martin, R. C., J. T. Thor, J. D. H. Lambert, P. Isabelle, H. D. Voldeng and D. L. Smith. 1989. Reduction of European corn borer (Lepidoptera: Pyralidae) damage by intercropping corn with soybean. J. Econ. Entomol. 82: 1455-1459.

Mathez, F. C. 1972. *Chilo partellus* Swinh.; *C. orichalcociliellus* Strand (Lepidoptera: Crambidae) and *Sesamia calamistis* Hmps (Lepidoptera: Noctuidae) on maize in the Coast Province, Kenya. Mitt. Schweiz. Ent. Ges. 45: 267-289.

Midmore, D. J. & J. Alcazar. 1991. Mixed planting of potato cultivars: growth, yield and leaf miner damage in the cool tropics. Exp. Agric. 27: 305-318.

Myers, N. 1980. The conversion of tropical forests. Environment 22: 6-13.

NAS. 1980. Firewood Crops: shrubs and tree species for energy production. National Academy of Sciences, Washington, D.C. 237 pp.

O'Sullivan, T. E. 1985. Farming systems and soil management: The Philippines/Australian development assistance program experience. *In* Craswell, E. T. Remenyi, L. V. and Nallana, L. G. (eds.), Soil erosion management, ACIAR Proceedings Series 6, pp. 77-81. ACIAR, Canberra, Australia.

Overholt, W. A., K. Ogedah and P. M. Lammers. 1994. Distribution and sampling of *Chilo partellus* (Lepidoptera: Pyralidae) in maize and sorghum on the Kenya coast. Bull. Ent. Res. 84: 367-378.

Päts, P. and B. Ekbom. 1992. Infestation and dispersal of early instars of *Chilo partellus* (Lepidoptera: Pyralidae) at different densities. Environ. Entomol. 21:1110-1113.

Päts, P. and B. Ekbom. 1994. Distribution of *Chilo partellus* (Lepidoptera: Pyralidae) egg batches on maize. J. Insect Behav. 17: 29-40.

Risch, S. J. 1980. The population dynamics of several herbivorous beetles in tropical agroecosystem: the effect of intercropping corn, beans, squash in Costa Rica. J. Appl. Ecol. 17: 593-612.

Risch, S. J. 1981. Insect herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. Ecology 62: 1325-1340.

Risch, S. J., D. Andow, and M. A. Altieri. 1983. Agroecosystem diversity and pest control: Data, tentative conclusions, and new research directions. Environ. Entomol. 12: 625-629.

Root, R. B. 1973. Organization of plant - arthropod association in simple and diverse habitats: The fauna of collards (*Brassicae olevaceae*). Ecol . Monogr. 43: 95-124.

Statistical Analysis Systems Institute Inc. 1985 SAS Users Guide. Statistics, Version 5 edn. SAS Institute Inc., Cary, NC.

Scheltez, P. 1978. Ecological and Physiological aspects of aestivation-diapause in the larvae of two pyralid stalk-borers of maize in Kenya. Landbouwhogeschool, Waginegen, The Netherlands, 110 pp.

Sombroek, W. G., H. M. H. Braun and B. J. A. Van Der Pouw. 1982. Exploratory soil map and agroclimatic zone map of Kenya. Kenya Soil Survey, Nairobi.

Suryatna, E. S. 1976. Nutrient uptake, insect disease, labour use, and productivity characteristics of selected traditional intercropping patterns which together affect their continued use by farmers. Ph.D. thesis, University of Philippines, Los Baños.

Szott, L. T. 1987. Improving the productivity of shifting cultivation in the Amazon Basin of Peru through use of leguminous vegetation. Ph.D. dissertation, North Carolina State University, Raleigh, NC, USA.

Tonhasca, A. Jr. & D. N. Byrne. 1994. The effects of crop diversification on herbivorous insects: a meta-analysis approach. Ecol. Entomol. 19: 239-244.

Vietmeyer, N. D. 1979. Tropical tree legumes: a front-line against deforestation. Ceres (71) 12, No. 5, pp. 38-41.

Warui, C. M and J. N. Kuria. 1983. Population incidence and the control of maize stalk-borers *Chilo partellus* (Swinh.), *C. orichalcociliellus* Strand and *Sesamia calamistis* Hmps, in Coast province, Kenya. Insect Sci. Applic. vol.4, No.1/2, pp. 11-18

Figure 2.1: Location of Mtwapa and Amoyo experimental field sites in Kenya

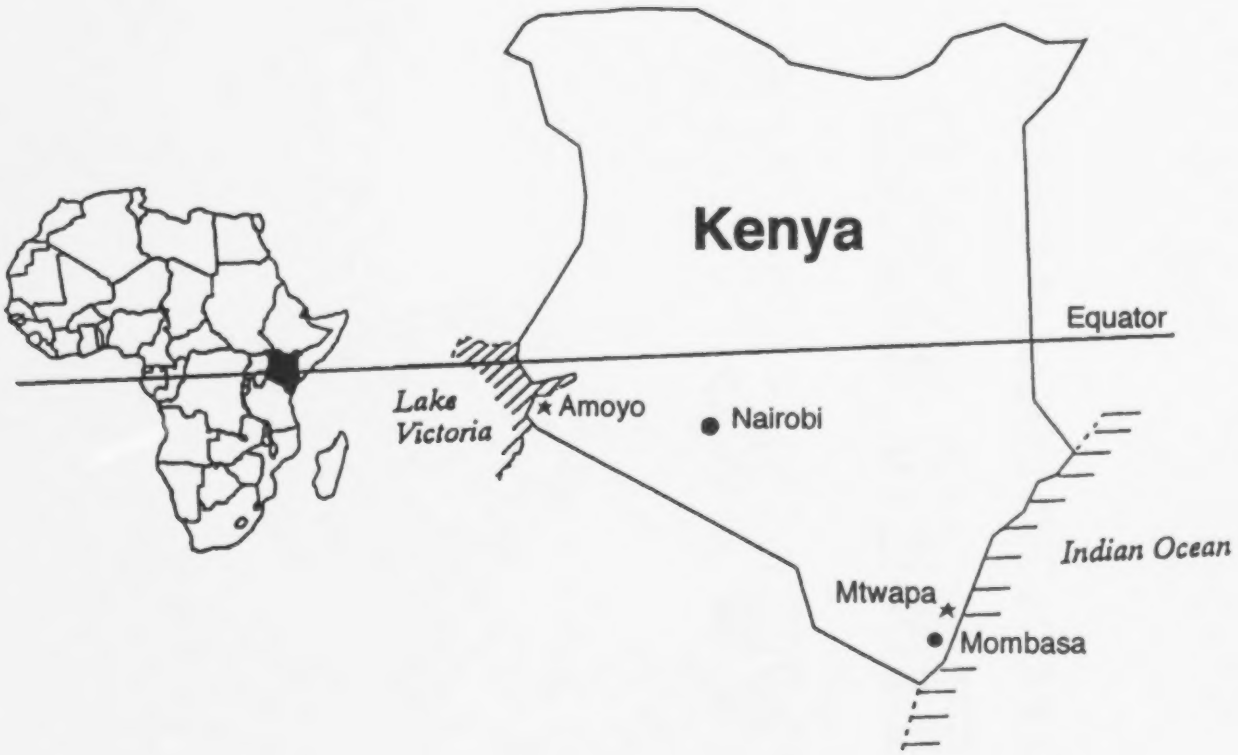
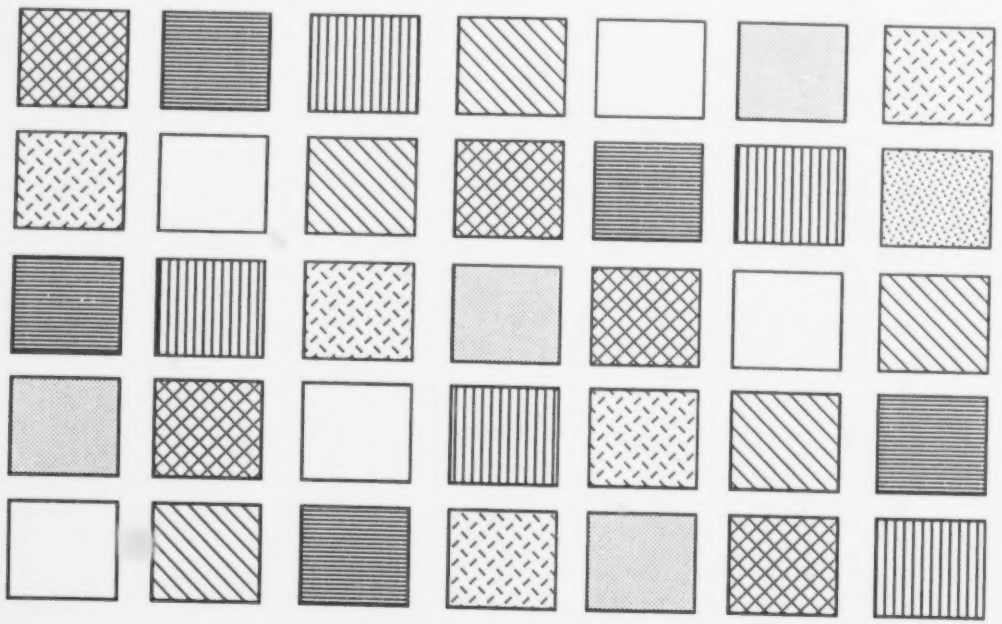


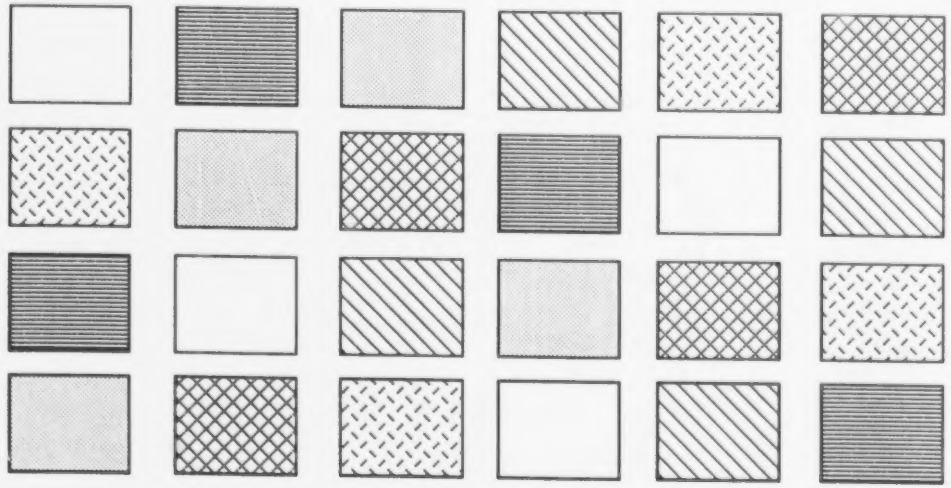
FIGURE 2.2: EXPERIMENTAL PLOT LAYOUT AT MTWAPA



LEGEND

- Maize monocrop
- 2.25m intercrop
- 2.25m unmulched intercrop
- 2.25m unweeded intercrop
- 1.5m intercrop
- 3.0m intercrop
- Leucaena monocrop

FIGURE 2.3: EXPERIMENTAL PLOT LAYOUT AT AMOYO



LEGEND

- Maize monocrop
- 2.25m intercrop
- 2.25m unmulched intercrop
- 2.25m unweeded intercrop
- 1.5m intercrop
- 3.0m intercrop

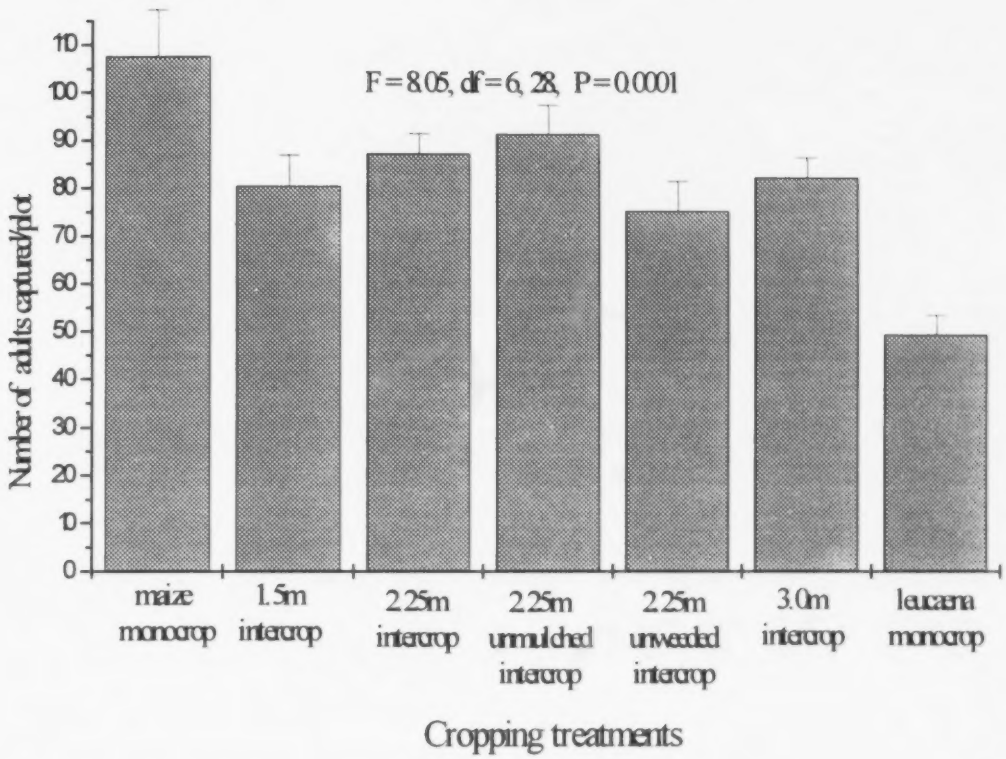


Figure 2.4: Total (±SE) number of *Chilo* spp adults captured per plot at Mtwapa. Data represent treatment totals over one year of trapping.

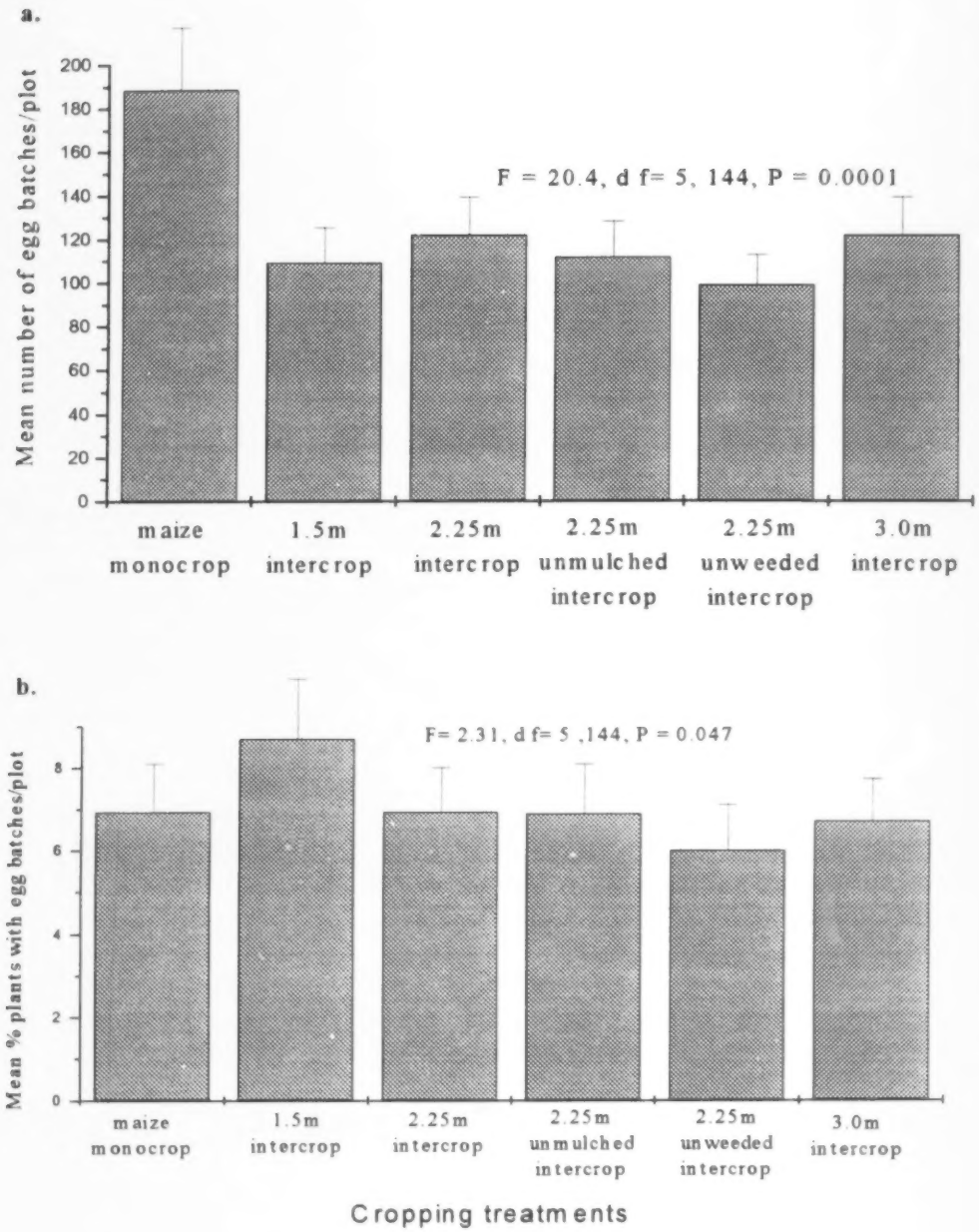
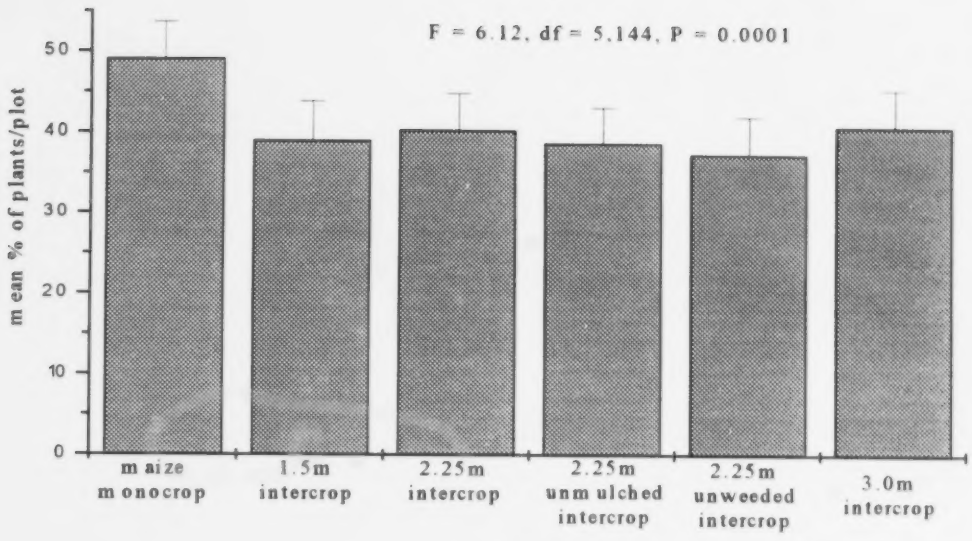


Figure 2.5: Incidence of *Chilo* spp egg batches at Mtwapa: a. Average (±SE) number of batches per plot, b. Average (±SE) percentage of plants with batches per plot. Means represent treatment averages over six cropping seasons.

a.


F = 6.12, df = 5,144, P = 0.0001
mean % of plants/plot
0
10
20
30
40
50
maize monocrop
1.5m intercrop
2.25m intercrop
2.25m unmulched intercrop
2.25m unweeded intercrop
3.0m intercrop

b.

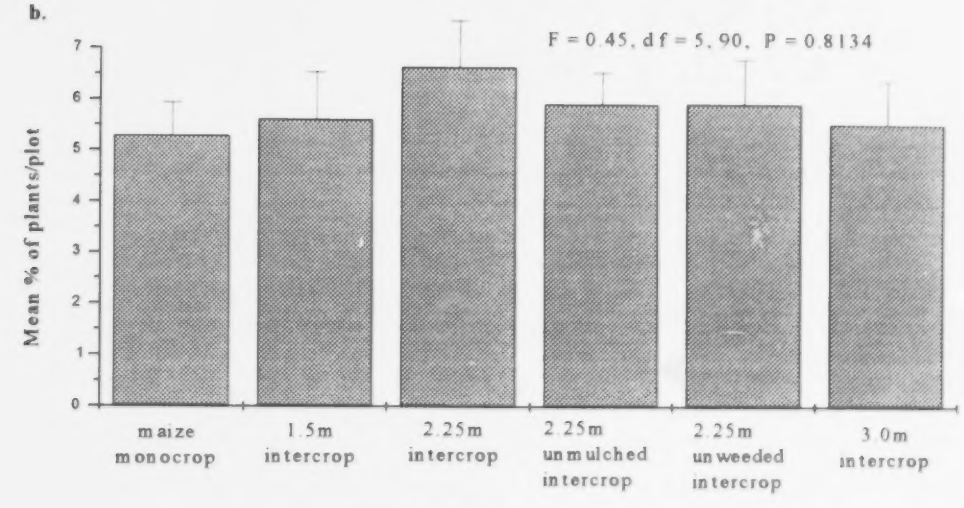

F = 0.45, df = 5, 90, P = 0.8134
Mean % of plants/plot
0
1
2
3
4
5
6
7
maize monocrop
1.5m intercrop
2.25m intercrop
2.25m unmulched intercrop
2.25m unweeded intercrop
3.0m intercrop
Cropping treatments

Figure 2.6: Average (±SE) percentage of maize plants with foliar damage per plot. Means represent treatment averages over six cropping seasons. a. Mtwapa b. Amoyo

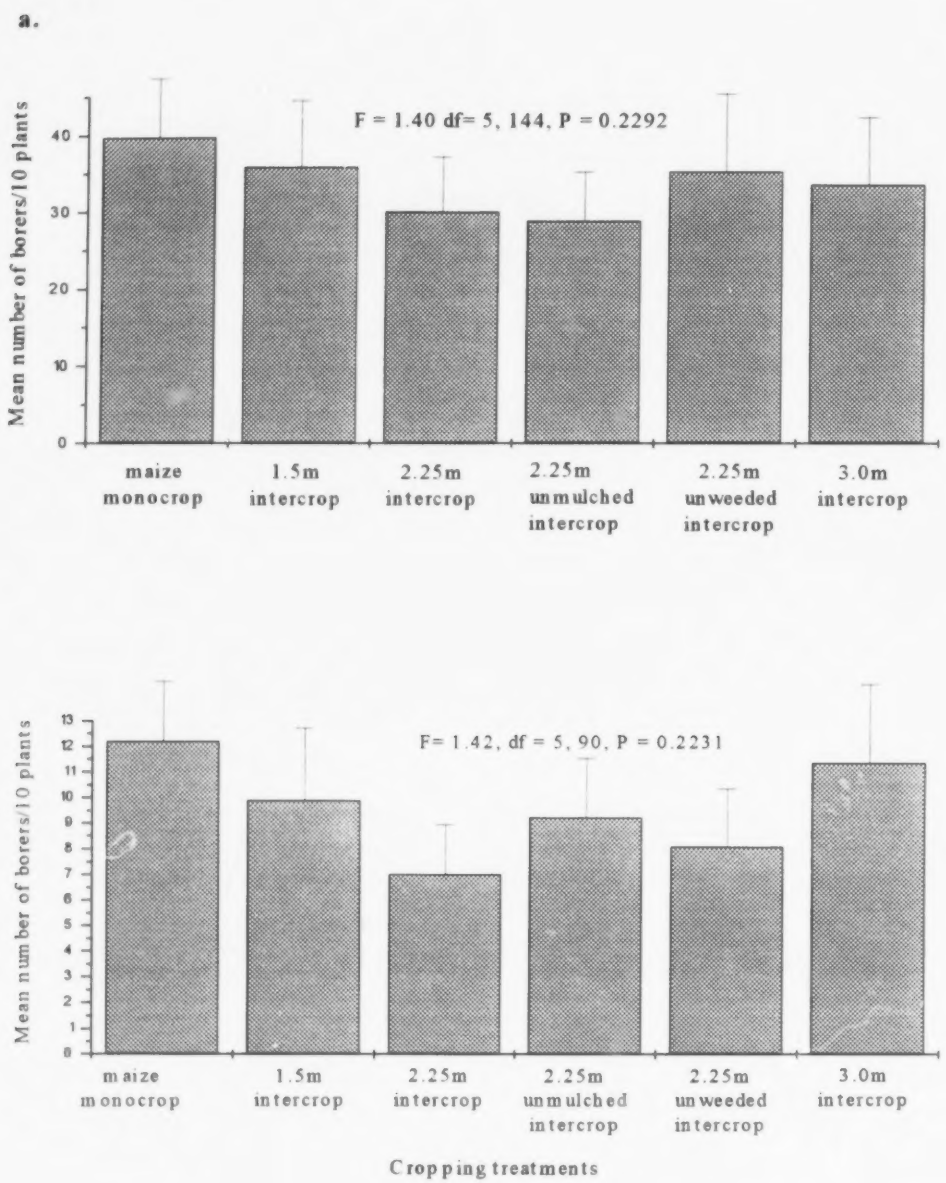


Figure 2.7: Average (±SE) number of stem borer larvae & pupae per 10 maize plants. Means represent treatment averages over six cropping seasons. a. Mtwapa b. Amoyo

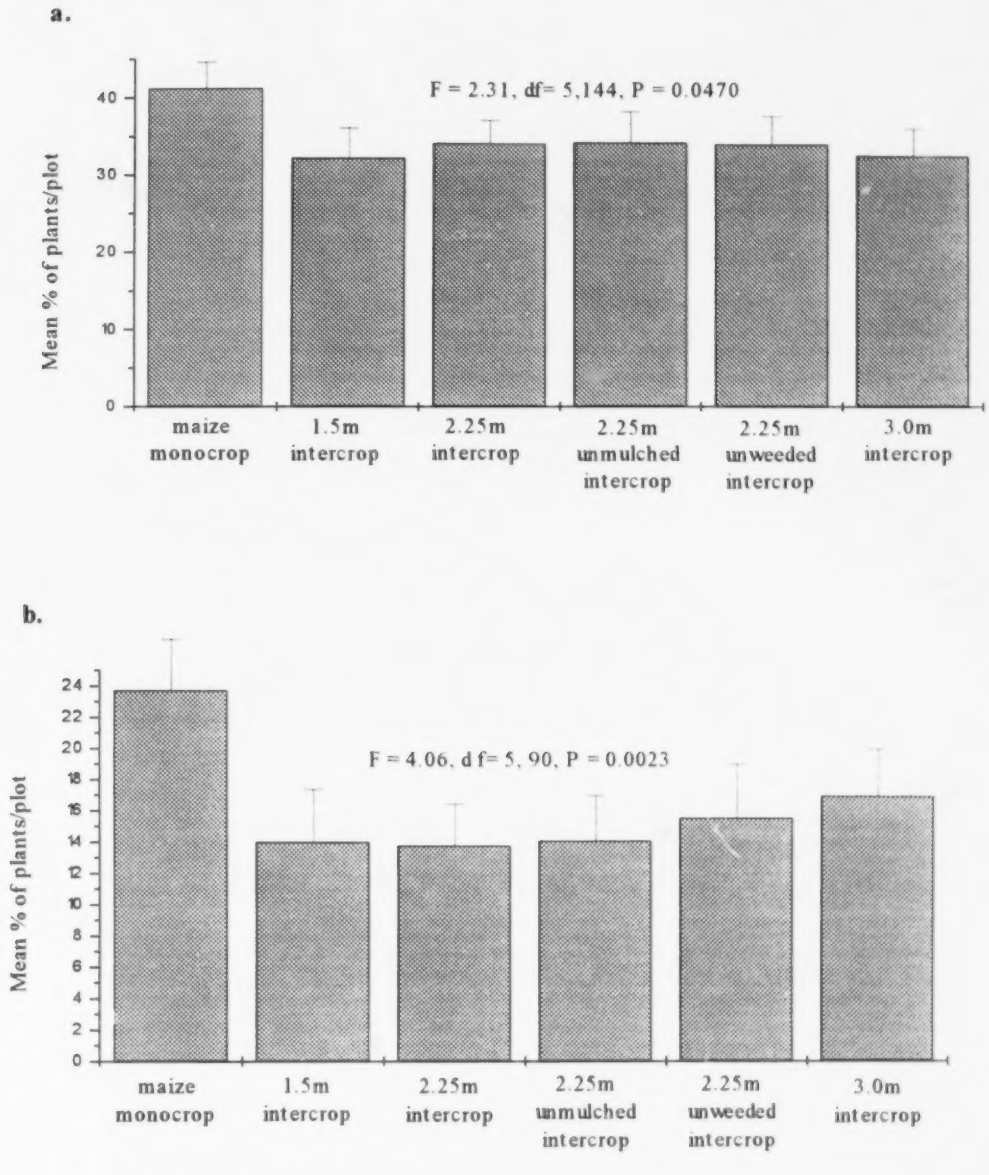


Figure 2.8: Average (±SE) percentage of maize plants with stem borer larvae and pupae/plot. Means represent treatment averages over six cropping seasons. a. Mtwapa b. Amoyo

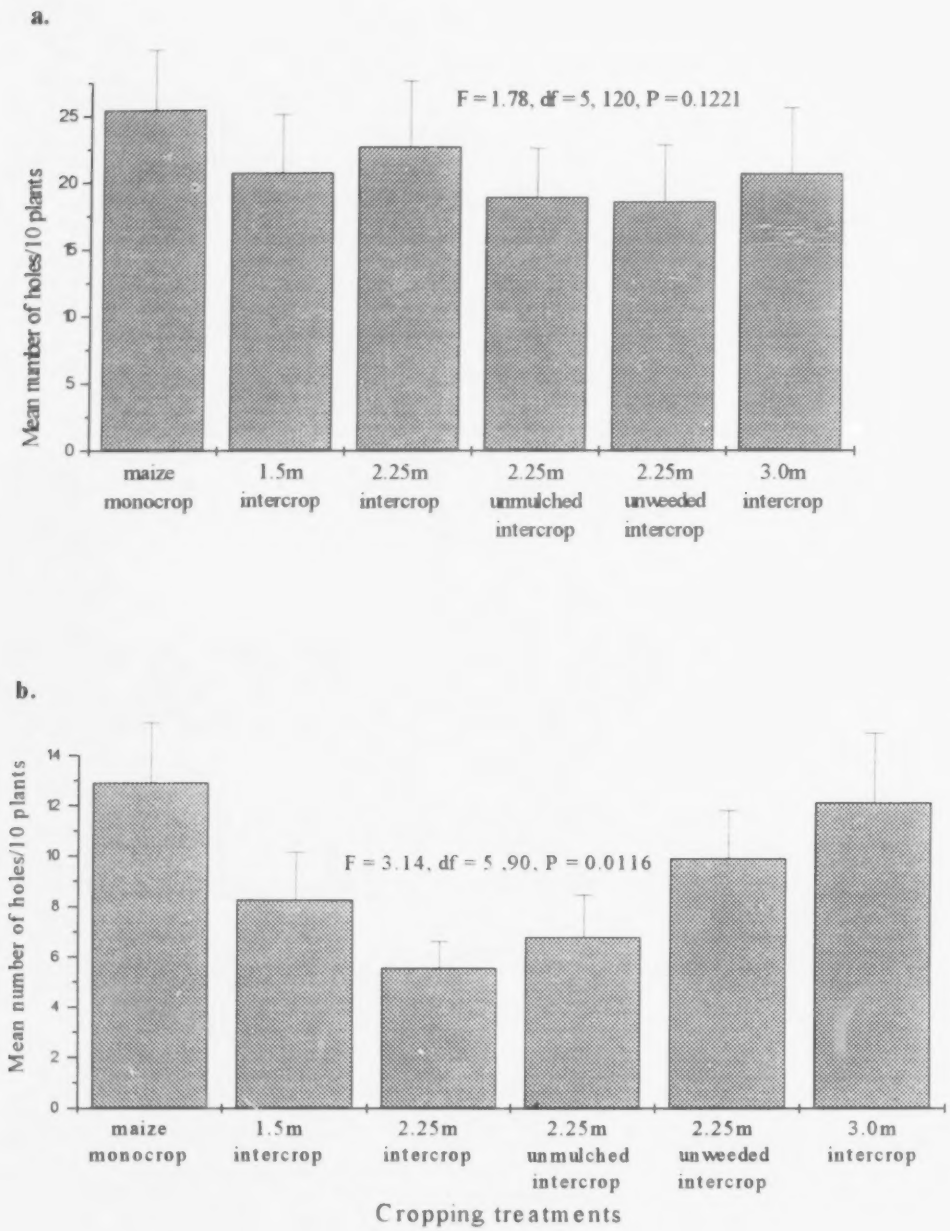


Figure 2.9: Average (±SE) number of stem borer exit or entry holes per 10 maize plants. Means represent treatment averages over six cropping seasons. a. Mtwapa b. Amoyo

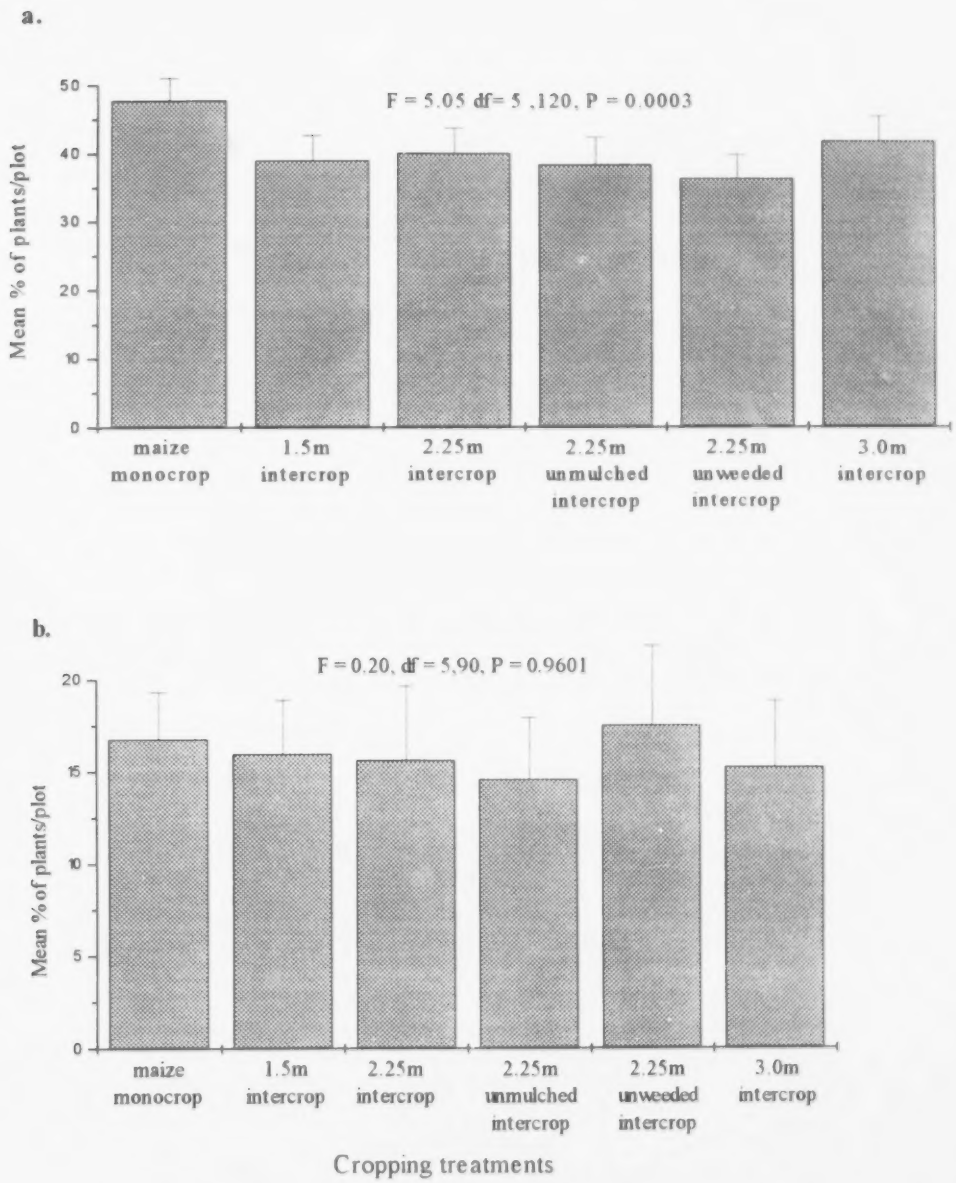


Figure 2.10: Average (±SE) percentage of plants with stem borer entry or exit holes per plot. Means represent treatment averages over cropping seasons. a. Mtwapa b. Amoyo

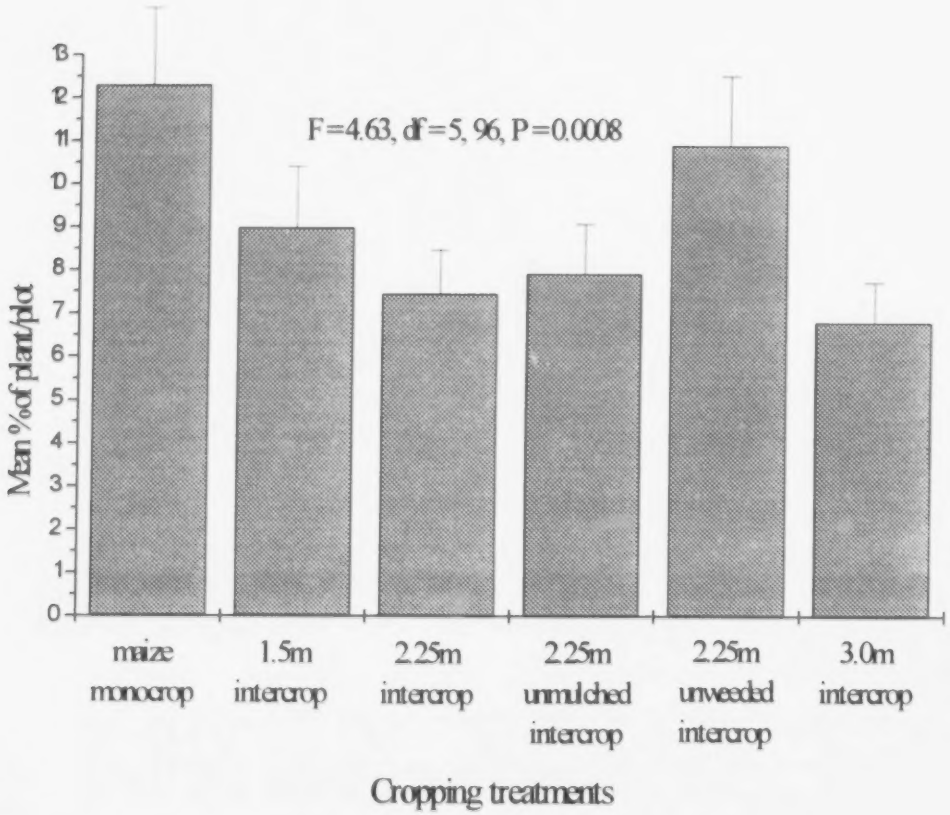


Figure 2.11: Average (±SE) percentage of maize plant mortality per plot at Mtwapa. Means represent treatment averages over cropping seasons.

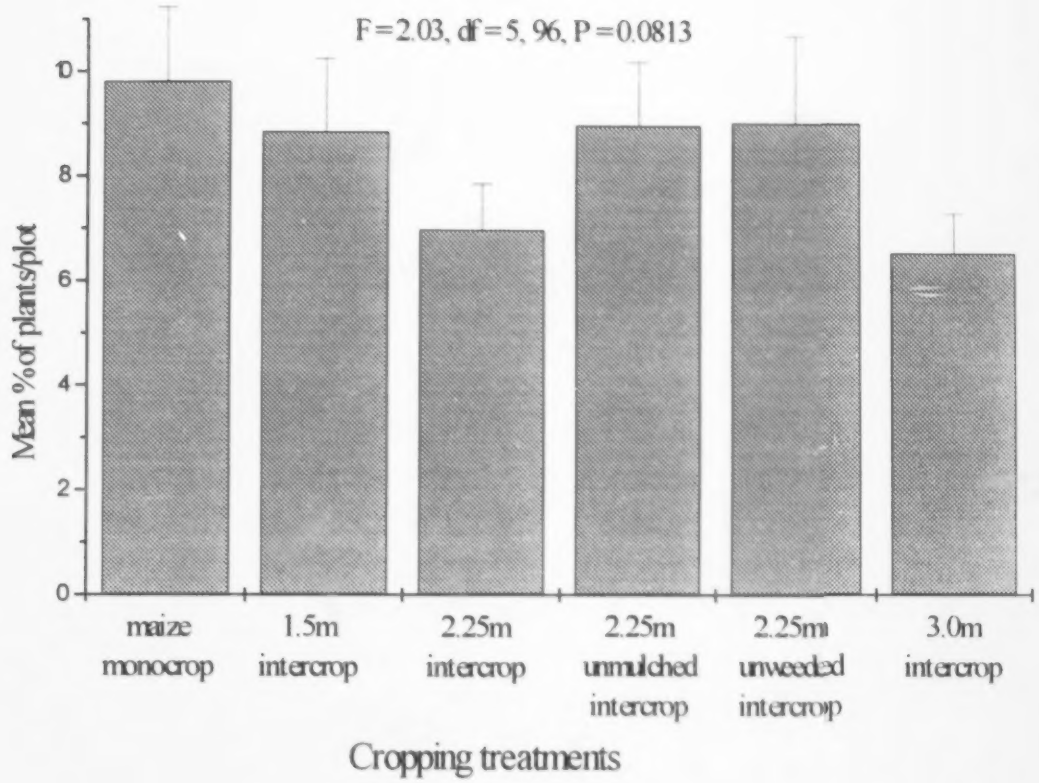


Figure 2.12: Average (±SE) percentage of maize plants with broken stems per plot at Mtwapa. Means represent treatment averages over cropping seasons.

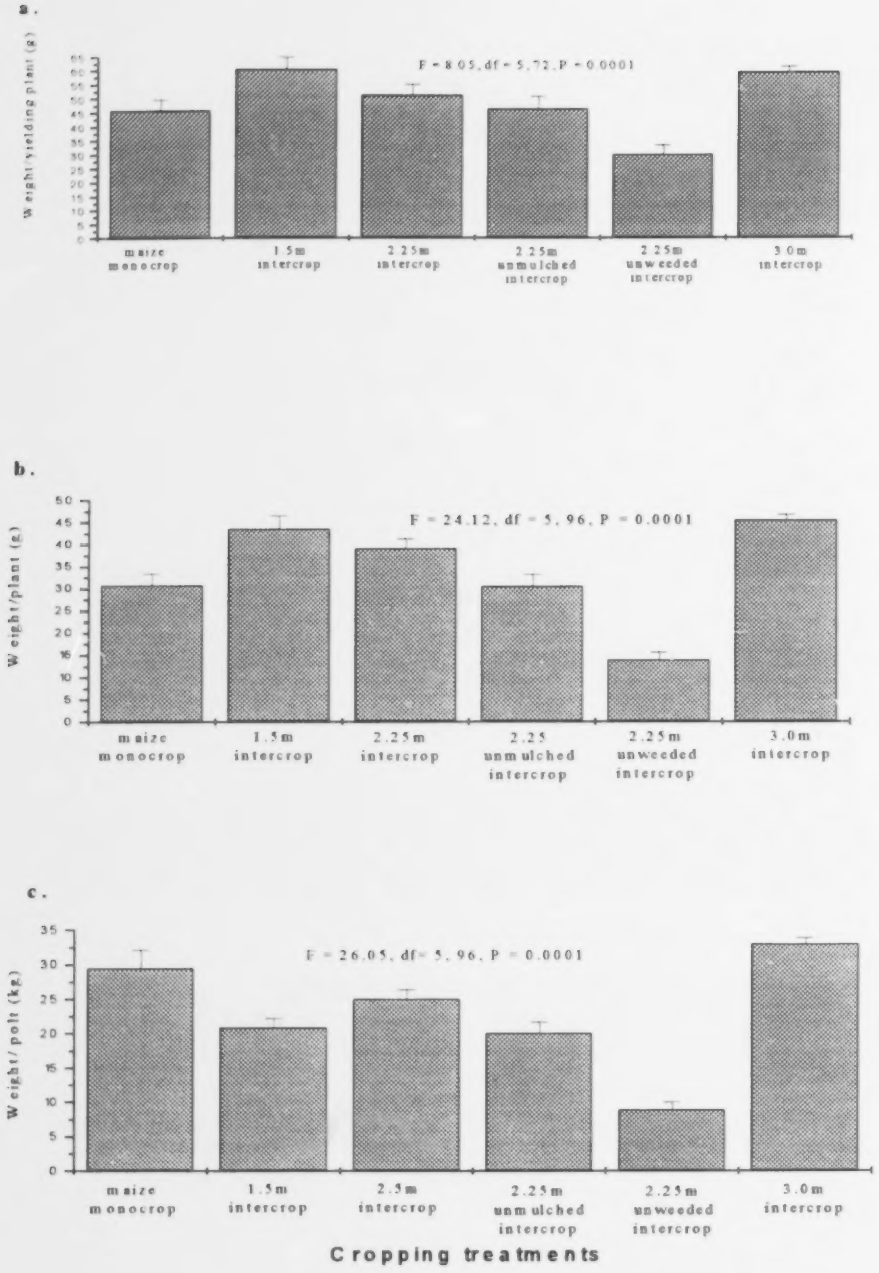


Figure 2.13: Average (±SE) yield of maize at Mtwapa: a. weight of seeds/yielding plant, b. weight of seeds/plant, c. weight of seeds/plot. Means represent treatment averages over cropping seasons.

Table 2.1. Summary of hedgerow spacing and treatments

Leucaena hedgerow spacing (m)	rows of maize between hedgerows	cultural treatments
1.5m (leucaena monoculture)	0	weeded/mulched
1.5m	1	weeded/mulched
2.25m	2	weeded/mulched
2.25m	2	weeded/unmulched
2.25m	2	unweeded/mulched
3.0m	3	weeded/mulched
Non (maize monocrop)	all	weeded/unmulched

Table 2.2. Summary of post-Analysis of Variance data analysis

Contrasts	Treatments
1. Non-host vs Host*	leucaena monocrop vs rest
2. Monocrop vs Intercrops	maize monocrop vs all intercrops
3. Weeds	2.25m unweeded intercrop vs 2.25m and 2.25m unmulched intercrops
4. Mulch	2.25m unmulched vs 2.25m intercrop
5. Spacing Regression analysis:	1.5m, 2.25m and 3.0m intercrops

* contrasted only for number of adult *Chilo spp.* captured

Table 2.3: Orthogonal comparisons for number of *Chilo spp* adults captured per plot at Mtwapa

Contrasts	P
leucaena monocrop vs rest	0.00
maize monocrop vs intercrops	0.00
weeded vs unweeded	0.08
mulched vs unmulched	0.64

Spacing regression analysis	R^2	P
linear	0.005	0.81
quadratic	0.066	0.37

Table 2.4a: Orthogonal comparisons for number of *Chilo spp.* egg batches per plot at Mtwapa

Contrasts	P
maize monocrop vs intercrops	0.00
weeded vs unweeded	0.04
mulched vs unmulched	0.03

Spacing regression analysis	R^2	P
linear	0.148	0.16
quadratic	0.043	0.44

Table 2.4b: Orthogonal comparisons for percentage of plants with egg batches at Mtwapa

Contrasts	P
maize monocrop vs intercrops	0.86
weeded vs unweeded	0.21
mulched vs unmulched	0.95

Spacing regression analysis	R^2	P
linear	0.366	0.02
quadratic	0.074	0.23

Table 2.5: Orthogonal comparisons for percentage of plants with foliar damage at Mtwapa and Amoyo

	Mtwapa		Amoyo	
Contrasts		P		P
maize monocrop vs intercrops		0.00		0.41
weeded vs unweeded		0.32		0.68
mulched vs unmulched		0.51		0.47
Spacing regression analysis	R^2	P	R^2	P
linear	0.057	0.41	0.000	0.97
quadratic	0.003	0.86	0.061	0.46

Table 2.6: Orthogonal comparisons for average number of borers per 10 plants at Mtwapa and Amoyo

	Mtwapa		Amoyo	
Contrasts		P		P
maize monocrop vs intercrops		0.06		0.09
weeded vs unweeded		0.16		0.99
mulched vs unmulched		0.80		0.34
Spacing regression analysis	R^2	P	R^2	P
linear	0.016	0.65	0.024	0.62
quadratic	0.093	0.29	0.190	0.17

Table 2.7: Orthogonal comparisons for percentage of plants with borers per plot at Mtwapa and Amoyo

	Mtwapa		Amoyo	
Contrasts		P		P
maize monocrop vs intercrops		0.00		0.00
weeded vs unweeded		0.93		0.26
mulched vs unmulched		0.96		0.90
Spacing regression analysis	R^2	P	R^2	P
linear	0.001	0.89	0.085	0.37
quadratic	0.084	0.32	0.039	0.54

Table 2.8: Orthogonal comparisons for number of stem borer entry and exit holes/10 plants at Mtwapa and Amoyo

	Mtwapa		Amoyo	
Contrasts		P		P
maize monocrop vs intercrops		0.03		0.02
weeded vs unweeded		0.37		0.07
mulched vs unmulched		0.18		0.60
Spacing regression analysis	R^2	P	R^2	P
linear	0.053	0.42	0.195	0.07
quadratic	0.016	0.66	0.384	0.02

Table 2.9: Orthogonal comparisons for percentage of plants with stem borer entry and exit holes/10 plants at Mtwapa and Amoyo

	Mtwapa		Amoyo	
Contrasts		P		P
maize monocrop vs intercrops		0.00		0.71
weeded vs unweeded		0.18		0.40
mulched vs unmulched		0.51		0.75
Spacing regression analysis	R^2	P	R^2	P
linear	0.186	0.14	0.006	0.83
quadratic	0.004	0.82	0.000	1.00

Table 2.10: Orthogonal comparisons for percentage of plants dead per plot at Mtwapa

Contrasts	P
maize monocrop vs intercrops	0.00
weeded vs unweeded	0.06
mulched vs unmulched	0.08

Spacing regression analysis	R^2	P
linear	0.237	0.08
quadratic	0.013	0.66

Table 2.11: Orthogonal comparisons for percentage of plants with broken stems at Mtwapa

Contrasts	P
maize monocrop vs intercrops	0.09
weeded vs unweeded	0.35
mulched vs unmulched	0.12

Spacing regression analysis	R^2	P
linear	0.240	0.07
quadratic	0.031	0.49

Table 2.12a: Orthogonal comparisons for weight of seeds per plant (plants with ears) at Mtwapa

Contrasts		P
maize monocrop vs intercrops		0.38
weeded vs unweeded		0.00
mulched vs unmulched		0.38
Spacing regression analysis	R^2	P
linear	0.002	0.86
quadratic	0.242	0.07

Table 2.12b: Orthogonal comparisons for weight of seeds/plant (all plants) at Mtwapa

Contrasts		P
maize monocrop vs intercrops		0.15
weeded vs unweeded		0.00
mulched vs unmulched		0.01
maize mono vs 1.25m,2.25m & 3.0m inter		0.00
maize monocrop vs unmulched		0.94
maize monocrop vs unweeded		0.00
Spacing regression analysis	R^2	P
linear	0.022	0.58
quadratic	0.164	0.15

Table 2.12c: Orthogonal comparisons for weight of seeds per plot at Mtwapa

Contrasts		P
maize monocrop vs intercrops		0.00
weeded vs unweeded		0.00
mulched vs unmulched		0.04
maize monocrop vs 3.0m intercrop		0.15
Spacing regression analysis	R^2	P
linear	0.664	0.00
quadratic	0.022	0.38

3. NATURAL ENEMY ABUNDANCE AND ACTIVITY IN THE MAIZE-LEUCAENA AGROFORESTRY SYSTEM

3.1 INTRODUCTION

The cultural practice of increasing vegetational diversity in agroecosystems increases system stability and decreases the incidence of major insect pest outbreaks in some monocultures (Perrin, 1977, 1980; Altieri and Letourneau, 1982; Risch 1983, Risch et al., 1983; Andow, 1991). Among the hypotheses proposed to explain these observations is, that vegetational diversity increases both population size and impacts of entomophagous natural enemies that regulate populations of herbivorous arthropod pests (Risch, 1983; Herzog and Funderburk, 1986; Russell, 1989, Andow, 1991). Root (1973) first proposed this 'Enemies Hypothesis' to explain the observed decrease in herbivore abundance in vegetationally diverse collard stands. Increases in abundance and diversity of arthropod predators and parasitoids are attributed largely to the increased availability of suitable microhabitats, and diverse food resources such as nectar, pollen, and alternate hosts or prey (Root 1973; Vandermeer, 1990). Such nutrient sources frequently result in increased longevity and fecundity of natural enemies, and these benefits may strengthen their functional and numerical responses (Price et al., 1980). The performance and effectiveness of natural enemies may also be enhanced by chemical cues from associated plants (Altieri et al., 1981; Nordland et al., 1988; Vet and Dicke, 1992; Potting et al., 1995).

Many studies of specific systems support the enemies hypothesis. Letourneau (1983) reported consistently higher captures of parasitoids and higher rates of parasitism of eggs and larvae of the squash feeding *Diaphania hyalinata* (Lepidoptera: Pyralidae) in squash-cowpea-maize polycultures than in squash monoculture in tropical Mexico. Brussel sprouts grown in polycultures with fava bean or wild mustard supported more species of natural enemies than monocultures (Altieri, 1984). Spiders were more effective against corn borers in a corn-groundnut intercrop than in a corn monoculture (Gavara and Raros, 1975). Altieri et al. (1977) and Speight and Lawton (1976) reported a higher incidence of

predators in a weedy crop than in comparable monocultures. Cárcamo and Spence (1994) showed experimentally that the predatory carabid *Pterostichus melanarius* was more attracted to barley-pea intercrop than to monocrops of barley, faba bean and fescue. Altieri et al. (1981) reported that parasitization rates of *Heliothis zea* eggs by *Trichogramma* species were higher in soybean-corn intercropped plots and weedy soybean plots than in weed-free soybean.

Conversely, reports abound that suggest variable response of natural enemies to vegetational diversity, with some species exhibiting neutral, or even negative responses, reflecting more the unpredictable tritrophic interactions between plants, herbivores and natural enemies. In a review of studies that tested the enemies hypothesis, nine found higher mortality rates in diverse systems, two found a lower mortality rate, and two found no difference (Russell, 1989). A recent review of the available literature revealed that of the 130 species of natural enemies encountered, 52.7% had higher densities on plants in polycultures, 9.3% were less abundant, 25.6 % had variable (inconsistent) response, while 13.2% showed no response (Andow, 1991). In many polycultural systems, the resource concentration and the impact of natural enemies seem to act in concert to reduce herbivore populations, but in others the effects of these phenomena may be antagonistic (Russell, 1989; Andow, 1991). It therefore appears that there is no 'rule of thumb' or general theory that globally predicts population size or activity of natural enemies in vegetationally diverse agroecosystems, and thus, each system must be evaluated individually (Nordland et al. 1984). This sort of situation generally results when the theoretical paradigm is simplistic and loosely linked to the appropriate parameters (Kingsland, 1995).

Agroforestry is a polycultural system in which trees are grown together with conventional agricultural crops. Although it is becoming increasingly popular, especially in the tropics, there are few studies that address how natural enemy populations are affected by agroforestry systems. The aim of my study was to examine the role and impact of enemies hypothesis on stem boring lepidopteran pests of maize in an agroforestry system involving alley cropping of maize and the tree legume *Leucaena leucocephala*. Alley cropping with leucaena sustains maize production (Kang et al., 1984) and can have significant positive impact on maize production particularly among the majority resource-

limited subsistent farmers of tropical Africa for whom maize is a staple food crop. It was expected that if the enemies hypothesis held, the increased natural enemy populations and activity in the maize-leucaena intercrop would provide greater level of protection from stem borers to the maize in the intercrop than in the monocrop. This could be a major contribution in the efforts towards the development of new environmentally safe, cost-effective and sustainable pest management methods for tropical Africa. This is essential because stem borers are often protected due to their boring activity, and are pervasive in the field throughout the growing season, making effective chemical control difficult and costly.

In these studies, I examined egg predation and parasitism, larval and pupal parasitism and mortality. Previous studies on life table analysis of the stem borer *Chilo partellus* on maize and sorghum under subsistence agriculture in Western Kenya showed that local predators and unidentified factors contributed up to 97.6% of generation mortality of the borers in the age interval from egg to early instar larvae, while parasitoids and pathogens contributed less than 1% mortality in the various life stages (Oloo, 1989). Parasitoid and pathogen induced mortality below 1% is very low considering that up to 100% pupal and 60-70% larval parasitism have been recorded for *Chilo partellus* in South Africa (Kfir, 1992). Thus, it appears that there is room available for improving natural enemy abundance and impacts in agroecosystems.

3.2 MATERIALS AND METHODS

3.2.1 Study site, experimental design and plot-layout

Information about the study site, general experimental design and plot-layout have been given in Chapter 2. A summary is given here. The study was carried out at the Kenya Agricultural Research Institute (KARI) Regional Research Centre at Mtwapa, Coast Province (3°56' S, 39°44' E and 15m above sea level), and at the Kenya Forestry Research Institute experimental field site at Amoyo, Nyanza Province (0°10' S, 34°23 E and approximately 1400m above sea level). Both sites have a bimodal rainfall with a long cropping season from April to June, and an often unreliable short cropping season between October to December. Experimental plots were laid out in a randomized

complete block design with five and four replications at Mtwapa and Amoyo respectively. Plots measured 18 x 12m at Mtwapa and 12x10m at Amoyo, separated by 6m buffer strips of bare ground. *Leucaena leucocephala* (Lam.) de Wit was planted in September 1992 in hedgerows at a spacing of 0.5m within hedgerows. Six of the plots at Mtwapa were randomly assigned between row spacings of 1.5m, 1.5m, 2.25m, 2.25m, 2.25m and 3.0m, while at Amoyo, five plots were assigned between row spacings of 1.5m, 2.25m, 2.25m, 2.25m and 3.0m. During the cropping season, maize was planted between hedgerows at a spacing of 30cm within rows and 75cm between rows. 1, 2 and 3 rows of maize were planted between hedgerows planted 1.5m, 2.25m and 3m apart respectively. One of the 1.5m plots at Mtwapa was not planted to maize (leucaena monocrop). A seventh plot at Mtwapa and a sixth at Amoyo was planted to maize alone (maize monocrop). During maize planting, trees were cut back to 30cm above ground. Plots were mulched with leucaena foliage except for one of the 2.25m plots, and regularly weeded except for another of the 2.25m plots.

3.2.2 Egg parasitism and predation and predator abundance

All the foliage of the maize plants at Mtwapa were carefully inspected for stem borer egg batches beginning 8 days after plant emergence during the cropping seasons of long and short rains of 1994 and long rains of 1995. All plants bearing egg batches were marked by a wooden peg in the soil. All unmarked plants were inspected again for freshly oviposited eggs 24 hours later. Ten batches of such eggs, each from a single plant were selected. The leaves bearing egg batches were tagged, while the position of each egg batch was marked with a permanent marker on the opposite leaf surface. On the third day, each egg batch was inspected and its condition recorded as healthy, partially eaten or missing. The ones missing or eaten were presumed to have been depredated. This data was expressed as percentage of eggs depredated per plot, and was collected only during the short rains of 1994 and long rains of 1995. All healthy and partially eaten eggs were cut out with some portion of leaf, placed in labeled vials, taken to the laboratory and observed until they hatched, parasitoids emerged, or failed to develop after two weeks. Data

obtained were expressed as percentage of eggs parasitized per plot. The procedure was repeated biweekly for 8 weeks.

In addition, at 5 and 7 weeks after plant emergence during the long rains of 1994, all plants per plot were inspected for eggs of a predatory *Chrysopa* sp. Personal observations revealed that the lacewing species fed upon stem borer eggs. All eggs and egg bearing plants were counted and data were expressed as number of *Chrysopa* sp. eggs per plot and percentage of plants with *Chrysopa* sp. eggs per plot respectively.

3.2.3 Larval and pupal parasitism

To test whether parasitoid abundance was affected by vegetation structure, larvae and pupae of *Chilo partellus* (Swinhoe), *Chilo orichalcociliellus* Strand, *Sesamia calamistis* (Hampson) and *Heliothis* sp. from field sampling (Chapter 2) were brought into the laboratory and kept individually in plastic containers perforated at the top for ventilation. The larvae were provided with fresh portions of maize stems for food up to the time they pupated or died. Similarly, pupae were kept until they emerged as adults or died. These were checked daily for the emergence of parasitoids. Parasitoids emerging from individual larvae or pupae were counted. Data obtained was expressed as percentage of borers parasitized per plot. The parasitoids were preserved in 70% alcohol and representatives sent to the International Centre for Insect Physiology and Ecology (ICIPE) for expert identification.

3.2.4 Larval and pupal mortality

In order to test for the possibility that action of microbial mortality agents might be affected by vegetation structure, dead larvae and pupae obtained from the same sampling program, and those that died while being held in the laboratory (see 3.2.3) were also counted. Larvae and pupae that showed symptoms of parasitization (exit holes on pupae or parasitoid pupal cases on or next to dead larvae) were excluded. Data obtained was expressed as percentage of stem borer larval and pupal mortality per plot. Stem borer populations were low at Amoyo, thus the study was only conducted at Mtwapa. No

further attempts were made to determine cause of death due to complexity of the necessary protocols involved in relation to facilities available.

3.2.5 Data Analysis

Data collected were averaged for individual plots during each cropping season because of the unequal frequency of samples taken during the seasons, and analyzed by two-way (treatment x seasons) analysis of variance (ANOVA) (PROC GLM, SAS Institute, 1985). Both actual and arcsine transformed data met the assumptions of ANOVA and were analyzed. Thereafter, pre-planned orthogonal comparisons were made to test for effects of intercropping, weeds and mulch. Regression analysis (PROC REG, SAS Institute, 1985) was used to test for linear and quadratic relationships of spacing on natural enemy activity and abundance variables.

3.3 RESULTS

3.3.1 Egg parasitism and predation and predator abundance

The proportion of eggs parasitized by *Trichogramma* species was generally high (> 77%) for all treatments (Figure 3.1). None of the pre-planned contrasts was significant except the inverse linear relationship between hedgerow spacing and rates of egg parasitism (Table 3.1), suggesting that the proportion of eggs parasitized decreased with increased hedgerow spacing or increased maize density.

The proportion of eggs depredated at Mtwapa ranged from 19.7 ± 5.78% - 44.5 ± 5.05% among treatments. A greater percentage of egg batches were predated or missing in the maize monocrop plot (Figure 3.2) and the *a priori* comparisons clearly show that egg depredation was significantly higher in the maize monocrop than in the intercropped plots (Table 3.2). There were no significant differences in predation between the unweeded plot and the weeded plots and between the unmulched plot and mulched plot. Similarly, there was no significant linear or quadratic relationship between spacing and the

percentage of egg batches predated, suggesting that spacing had no effect on egg predation.

Neither did the mean number of *Chrysopa* species eggs per plot and percentage of plants with *Chrysopa* species eggs per plot differ significantly among treatments in the overall ANOVAS, nor did the *a priori* contrasts indicate that vegetation structure or cultural treatment influenced the oviposition preference of *Chrysopa* species.

3.3.2 Larval and pupal parasitism

At Mtwapa, mean rates of parasitism ranged from 1.4 ± 1.39% - 17.6 ± 8.86% among treatments (Figure 3.3a). Eight larval and one pupal parasitoid species were found to parasitize the stem borers *Chilo partellus* and *Chilo orichalcociliellus*, while *Sesamia calamistis* was parasitized only by the larval endoparasitoid *Cotesia sesamiae* (Table 3.3). *C. sesamiae* accounted for 66% of the parasitism while the introduced *Cotesia flavipes* accounted for only 3.1%. Larval parasitism accounted for 91.8% of the parasitism while pupal parasitism accounted for the remaining 8.2%. Analysis of data on the percentage of larvae and pupae parasitized per plot (Table 3.4) indicate that there were no significant differences among treatments, suggesting that vegetation structure and cultural treatments had no consistent effect on parasitism.

At Amoyo, mean rates of parasitism ranged from 2.8 ± 1.11% - 10.1 ± 5.28% among treatments (Figure 3.3b). Five larval, one pupal, and one larval hyperparasitoid species were found to parasitize the stem borer *Chilo partellus* and *Heliothis* species. (Table 3.3). The introduced *C. flavipes* parasitized only *C. partellus*. *Cotesia* species was the most predominant and accounted for 35% of the parasitism while the introduced *C. flavipes* accounted for 15%. Larval parasitism was responsible for 90 % of the parasitism, pupal parasitism 5% and, hyperparasitism 5%. A greater percentage of larvae and pupae were parasitized in the maize monocrop plot (Figure 3.3b), and the *a priori* comparisons indicate that the percentage was significantly higher in the maize monocrop than in the intercropped plots (Table 3.4). The contrasts further suggest that there were no significant

differences between the unweeded plot and the weeded plots and between the unmulched plot and mulched plot. However, there was significant linear relationship between spacing and number of eggs oviposited, suggesting that larval and pupal parasitism increased with increasing hedgerow spacing.

3.3.3 Larval and pupal mortality

Mean larval and pupal mortality at Mtwapa ranged from 17.6 ± 3.26% - 24.1 ± 7.45% among treatments (Figure 3.4). Most larval cadavers recovered had a common characteristic dark coloration of the entire body, suggesting that mortality could be associated with particular type of causative agent, most probably microbial agents. The maize monocrop and the unmulched plots had the lowest incidence of larval mortality However statistical analysis showed that the differences among treatment plots were not significant. The *a priori* contrasts (Table 3.5) did not differ significantly, clearly indicating that vegetation structure and cultural treatments had no consistent influence on the prevalence and efficacy of the presumptive microbial entomopathogens.

3.4: DISCUSSION AND CONCLUSIONS

3.4.1 Parasitism

I found no evidence for the operation of the enemies hypothesis with regards to parasitism. Mean rates of egg and larval/pupal parasitism at Mtwapa did not differ significantly among treatments, indicating that use of the maize-leucaena agroforestry system did not promote colonization and activity of stem borer parasitoids. On the other hand, rates of larval/pupal parasitism at Amoyo were significantly higher in the maize monocrop than in the maize-leucaena intercrops, suggesting that response to the enemies hypothesis may vary with location. Rates of egg parasitism at Mtwapa decreased with increasing leucaena hedgerow spacing while the converse occurred with larval/pupal parasitism at Amoyo. However these rates were not affected by weeds and mulch. Thus, Root's (1973) enemies hypothesis that natural enemies will be more abundant in

polycultures than in monocultures was not supported at Mtwapa (neutral response) and contradicted at Amoyo. My results are consistent with that of Williams et al. (1995) who reported that rates of larval parasitism of the green cloverworm were not significantly different between monocropped soybean and soybean intercropped with sorghum. Similarly, studies by Pavuk and Barret (1993) also reported a neutral response to agroecosystem diversification by larval parasitoids of the green cloverworm.

Most studies that have supported the enemies hypothesis have involved mainly generalist natural enemies (Sheehan, 1986; Russell, 1989). The enemies hypothesis may better explain population level responses of generalist than specialist enemies because the provision of alternative food and microhabitats associated with diverse vegetation are more relevant to enemies with broad feeding ranges than to specialist enemies (Sheehan, 1986). Thus, most parasitoids which commonly specialize in host use other than flowers, may not benefit from vegetationally diverse agroecosystems.

Plants have evolved numerous characteristics to defend themselves against herbivore attack (Juniper and Southwood, 1986; Tallamy and Raupp, 1991). Most interesting in the present context are indirect defenses mustered by plants that may promote the effectiveness of natural enemies of their herbivores (Price et al., 1980; Dicke and Sabelis, 1988). There is evidence that plants are actively involved in the release of chemical signals that attract natural enemies of their herbivores (Vinson, 1976, 1984; Dicke, 1994). It has been demonstrated for example, that when maize plant is injured by the stem boring *Chilo partellus*, the whole plant emits chemical signals (synomones) that attract its larval parasitoid *Cotesia flavipes* (Hymenoptera: Braconidae) (Potting et al., 1995), and that female *C. flavipes* can discriminate between odours emitted by uninfested and stem borer-infested maize plants (Potting et al., 1993). It is therefore conceivable that the impact of specialist natural enemies, could be diminished in diverse agroecosystems because chemical cues used in host finding may be disrupted by the presence of other chemicals from the companion plants, implying that the specialist natural enemies may be less able locating hosts to parasitize or feed upon in polycultures, as suggested by Price et al. (1980), Sheehan (1986), and Andow and Prokrym (1990). Price et al. (1980) called

this interference of host attractiveness of plants to natural enemies (and herbivores) by associated plants 'associational resistance'.

3.4.2 Predation

A greater proportion of eggs were depredated in the maize monocrop than in the intercrops, in contradiction to the enemies hypothesis. Similarly, both the numbers of *Chrysopa* eggs and the proportion of plants with *Chrysopa* eggs exhibited a neutral response to the hypothesis. My results are consistent with others which reported that predation rates on egg masses of the European corn borer *Ostrinia nubilalis* by a predaceous beetle *Coleomegilla maculata* were significantly higher in maize monocultures than in the more densely planted maize/bean/squash polyculture (Risch et al., 1983; Andow and Risch, 1985). Moreover, a review of the enemies hypothesis reported that 9.3% of the species studied had lower densities in polycultures while 13.2% did not show any difference (Andow, 1991).

Price et al. (1980) emphasized the importance of tritrophic level interactions in multispecies crop associations. They argued that herbivore/enemy interaction on one plant species can be influenced both by the presence of associated plants *per se*, and also by other herbivores present on the associated plant. This is a plausible explanation to the trend observed in my studies where egg predators commonly encountered but not sampled for various reasons, consisted of generalists like earwigs (Dermaptera: Forficulidae), ladybirds (Coleoptera: Coccinellidae), green lacewing adults (Neuroptera: Chrysopidae), and ants (Hymenoptera: Formicidae). These sorts of predators would have found the eggs, nymphal and adult stages of the leucaena psyllid *Heteropsylla cubana* (Homoptera: Psyllidae), which often occurred in high numbers on leucaena foliage throughout the growing season (see Chapter 4), more predictable and rewarding as prey/food because of their abundance and accessibility. Such predators were likely to spend less time searching and therefore be less effective in locating and depredating on stem borer eggs in the intercrop than in the monocrop. Similar opinion was expressed by Ables et al. (1978) who suggested that greater availability of alternative food sources may reduce predation rate in a target prey population.

3.4.3 Stem borer larval mortality

It was not possible to determine the cause of mortality due to expertise and logistical limitations. Nonetheless, the presumed pathogen-associated stem borer mortality did not differ significantly between treatments, and therefore exhibited a neutral response to the enemies hypothesis. A survey conducted to determine the prevalence of microorganisms in cereal stem borers and legume pod borers in western Kenya and coastal Kenya reported the presence of pathogenic microorganisms in all pest species sampled, including the maize stem borers *C. partellus*, *C. orichalcociliellus* and *S. calamistis* (Odindo et al., 1989). Bacteria and fungi were the most prevalent and accounted for 62.2% and 27% of the microorganisms obtained respectively. I therefore suspect that entomophagous pathogens must have accounted for a significant proportion of larval mortality.

There is paucity of studies or reviews that have examined the role of insect pathogens in the context of the enemies hypothesis. Nevertheless, my results are consistent with that of Williams et al. (1995) who reported that the incidence of the entomopathogenic fungus *Nomuraea rileyi* (Farlow) Sampson was not significantly different between green cloverworms in a monocropped soybean and those in soybean intercropped with sorghum. The denser hedgerow spaced plots might be expected to promote action of pathogens by providing a sheltered microclimate caused by the covering effect of the accompanying leucaena trees. A similar phenomenon has been observed on the incidence of *N. rileyi* where epizootics appear to be correlated with changes in microclimate, particularly increased humidity associated with soybean canopy closure (Sprenkel et al., 1979; Thorvilson et al., 1985). However, considering that stem borers spend most of their time concealed within stems where climatic variables like humidity and temperature would be minimally affected by external microclimatic conditions, the incidence of pathogens are expected to remain fairly uniform regardless of vegetation structure.

3.4.4 Conclusions

These studies show that alley cropping leucaena with maize did not increase, and in certain cases, reduced the abundance and/or activity of the natural enemies of maize stem borers. Therefore, my studies do not support the enemies hypothesis and the notion that vegetational diversity leads to increased abundance and activity of natural enemies does not generalize to this agroforestry system. Unfortunately, there is no present theory that predicts when natural enemies will exert significant mortality in polycultures (Andow, 1991) and thus, each case must be considered individually. Studies of the enemies hypothesis should address the possible effects of multitrophic interactions, and the influence of interceding abiotic factors within each system. The information thus generated may lead to a better understanding of the relative importance of various factors that control enemy populations, responses and effectiveness in polycultures, and move us towards a more predictive general theory of enemy activity in diverse systems.

3.5 REFERENCES

Ables, J. R., .S. L. Jones and D. W. McCommas. 1978. Response of selected predator species to different densities of *Aphis gossypii* and *Heliothis virescens* eggs. Environ. Entomol. 7: 402-404.

Altieri, M. A. 1984. Patterns of insect diversity in monocultures and polycultures of brussels sprouts. Prot. Ecol. 6: 227-232.

Altieri, M. A. and D. K. Letourneau. 1982. Vegetation management and biological control in agroecosystems. Crop Prot. 1: 405-430.

Altieri, M. A., A. van Schoonhoven and J. D. Doll. 1977. The ecological role of weeds on insect pest management systems: A review illustrated with bean (*Phaseolus vulgaris* L.) cropping systems. Agron. J. 75: 1005-1009.

Altieri, M. A., W. J. Lewis, D. A. Nordland, R. C. Gueldner, and J. W Todd. 1981. Chemical interactions between plants and *Trichogramma* sp. wasps in Georgia soybean fields. Prot. Ecol. 3: 259-263.

Andow, D. A. 1991. Vegetational diversity and arthropod population response. Ann. Rev. Entomol. 36: 561-586.

Andow, D. A. and S. J. Risch. 1985. Predation in diversified agroecosystems: relations between a coccinellid predator and its food. J. Appl. Ecol. 22: 357-72.

Andow, D. A. and D. R. Prokrym. 1990. Plant structural complexity and host finding by a parasitoid. Oecologia 82: 162-165.

Cárcamo, H. A. and J. R Spence. 1994. Crop type effects on the activity and distribution of ground beetles (Coleoptera: Carabidae). Environ. Entomol. 23: 684-692.

Dicke, M. 1994. Local and systemic production of volatile herbivore-induced terpenoids: their role in plant-carnivore mutualism. J. Plant Physiology 143: 465-472.

Dicke, M. and M. W. Sabelis. 1988. How plants obtain predatory mites as body guards. Neth. J. Zool. 38: 148-165.

Gavara, M. R. and R. S. Raros. 1975. Studies on the biology of the predatory wolf spider, *Lycosa pseudoannulata* Boes et Str (Aranadae: Lycosidae). Philippines Entomology 2: 427-444.

Herzog, D. C. and J. E. Funderburk. 1986. Ecological bases for habitat management and pest control. *In* M. Kogan (ed.), Ecological theory and integrated pest management practice. Wiley, New York. pp. 217-250.

Juniper, B. E and T. R. E. Southwood. 1986. Insects and the plant surface. Edward Arnold, London.

Kang, B. T., G. F. Wilson and T. L. Wilson. 1984. Alley cropping: a stable alternative to shifting cultivation. IITA, Ibadan, Nigeria.

Kfir, R. 1992. Seasonal abundance of the stem borer *Chilo partellus* (Lepidoptera: Pyralidae) and its parasites on summer grain crops. J. Econ. Entomol. 85: 518-529.

Kingsland, S. E. 1985. Modeling nature: episodes in the history of population ecology. Univ of Chicago Press, Chicago, IL. 267pp.

Letourneau, D. K. 1983. The effects of vegetational diversity on herbaceous insects and associated natural enemies: examples from tropical and temperate agroecosystems. Ph.D. dissertation, Univ. of CA, Berkeley.

Nordland, D. A., R. B. Chalfant and W. J. Lewis. 1984. Arthropod populations, yield and damage in monocultures and polycultures of corn, beans and tomatoes. Agric. Ecosyst. Environ. 11: 353-367.

Nordland, D. A., W. J. Lewis and M. A. Altieri. 1988. Influences of plant produced allelochemicals on the host and prey selection behavior of entomophagous insects. *In* P. Barbosa and D. K. Letourneau (eds.), Novel aspects of insect-plant interactions. John Wiley and Sons, New York.

Odindo, M. O.; W. A. Otieno, G. W. Oloo, J. Kilori and R. C. Odhiambo. 1989. Prevalence of microorganisms in field-sampled borers on sorghum, maize, and cowpea in western Kenya. Insect Sci. Applic. 10: 225-228.

Oloo, G. W. 1989. The role of local natural enemies in population dynamics of *Chilo partellus* (Swinh.) (Pyralidae) under subsistence farming systems in Kenya. Insect Sci. Applic. 10: 243-251.

Pavuk, D. M. and G. W. Barret. 1993. Influence of successional and grassy corridors on parasitism of *Plathypena scabra* (F.) (Lepidoptera: Noctuidae) larvae in soybean agroecosystems. Environ. Entomol. 22: 541-546.

Perrin, R. M. 1977. Pest management in multiple cropping systems. Agroecosystems 3: 93-118.

Perrin, R. M. 1980. The role of environmental diversity in crop protection. Prot. Ecol. 2: 77-114.

Potting, R. P. J., F. Osae-Danso, W . A. Overholt and A. J. Ngi-Song. 1993. Host selection in *Cotesia flavipes*, parasitoid of tropical stem borers. Proc. Exp. Appl. Entomol. 4:47-52.

Potting, R. J., E. M. Louise and Dicke, M. 1995. Host microhabitat location by stem-borer parasitoid *Cotesia flavipes*: The role of herbivore volatiles and locally and systemically induced plant volatiles. J. Chem. Ecol. 21: 525-539.

Price, P. W., C. E. Bouton, P. Gross, B. A. McPheron, J. N. Thompson and A. E. Weis. 1980. Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. Ann. Rev. Ecol. Syst. 11: 41-65.

Risch, S. J. 1983. Intercropping as a cultural pest control: prospects and limitations. Environ. Manage. 7: 9-14.

Risch, S. J., D. Andow, and M. A. Altieri. 1983. Agroecosystem diversity and pest control: data, tentative conclusions, and new research directions. Environ. Entomol. 12: 625-629.

Root, R. B. 1973. Organization of plant - arthropod association in simple and diverse habitats: The fauna of collards (*Brassicae olevaceae*). Ecol . Monogr. 43: 95-124.

Russell, E. P. 1989. Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. Environ. Entomol. 18: 590-599.

Statistical Analysis Systems Institute Inc. 1985 SAS Users Guide. Statistics, Version 5 edn. SAS Institute Inc., Cary, NC.

Sheehan, W. 1986. Response by specialist and generalist natural enemies to agroecosystem diversification: a selective review. Environ. Entomol. 15: 456-461.

Speight, M. R. and J. H. Lawton. 1976. The influence of weed cover on the mortality imposed on artificial prey by predatory ground beetles in cereal fields. Oecologia (Berl.) 23: 211-233.

Sprenkel, R. K., W. M. Brooks, J. W. Van Duyn and L. L. Dietz. 1979. The effects of three cultural variables on the incidence of *Nomuraeae rileyi*, phytophagous Lepidoptera, and their predators on soybeans. Environ. Entomol. 8: 334-339.

Tallamy, D. W. and M. J. Raupp (eds.). 1991. Phytochemical induction of herbivores. John Wiley and Sons, New York.

Thorvilson, H. G., L. P. Pedigo and L. C. Lewis. 1985. *Plathypena scabra* (F) (Lepidoptera: Noctuidae) populations and the incidence of natural enemies in four soybean tillage systems. J. Econ. Entomol. 78: 213-218.

Vandermeer, J. H. 1990. Intercropping. *In* C. R. Carrol, J. H. Vandermeer and P. M. Rosset (eds.), Agroecology. McGraw Hill, New York. pp. 481-516.

Vet, L. E. M. and M, Dicke. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. Annu. Rev. Entomol. 37: 141-172.

Vinson, S. B. 1976. Host selection by insect parasitoids. Annu. Rev. Entomol. 21: 109-133.

Vinson, S. B. 1984. Parasitoid-Host relationship. *In* W. J. Bell and R. T. Cardé (eds.), Chemical ecology of insects. Sinauer, Sunderland, Mass. pp. 205-233.

Williams, C. E., D. M. Pavuk, D. H. Taylor and T. H. Martin. 1995. Parasitism and disease incidence in the green cloverworm (Lepidoptera: Noctuidae) in strip-intercropped soybean agroecosystems. Environ. Entomol. 24: 253-260.

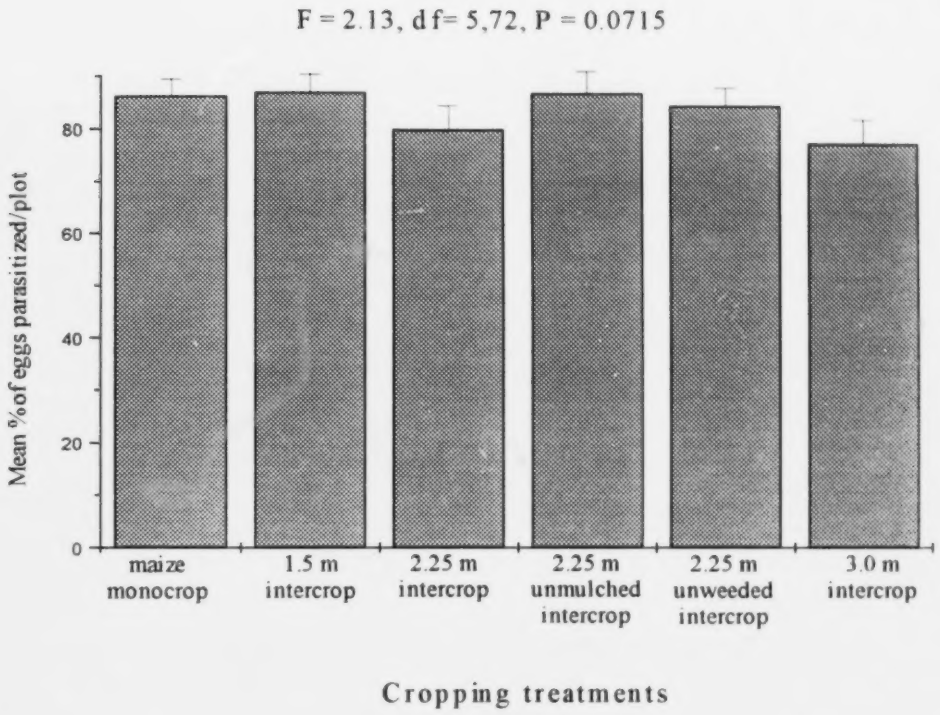


Figure 3.1: Average (±SE) percentage of stem borer eggs parasitized per plot at Mtwapa. Means represent treatment averages over three cropping seasons.

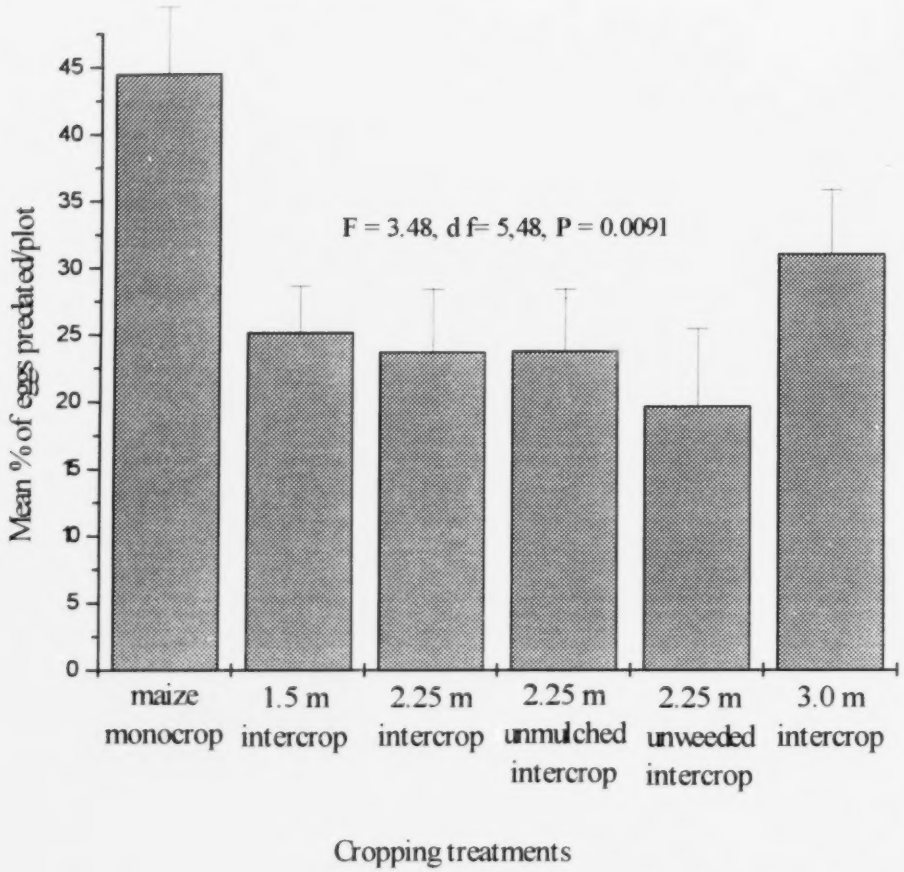


Figure 3.2: Average (±SE) percentage of stem borer eggs preyed upon per plot at Mtwapa. Means represent treatment averages over two cropping seasons.

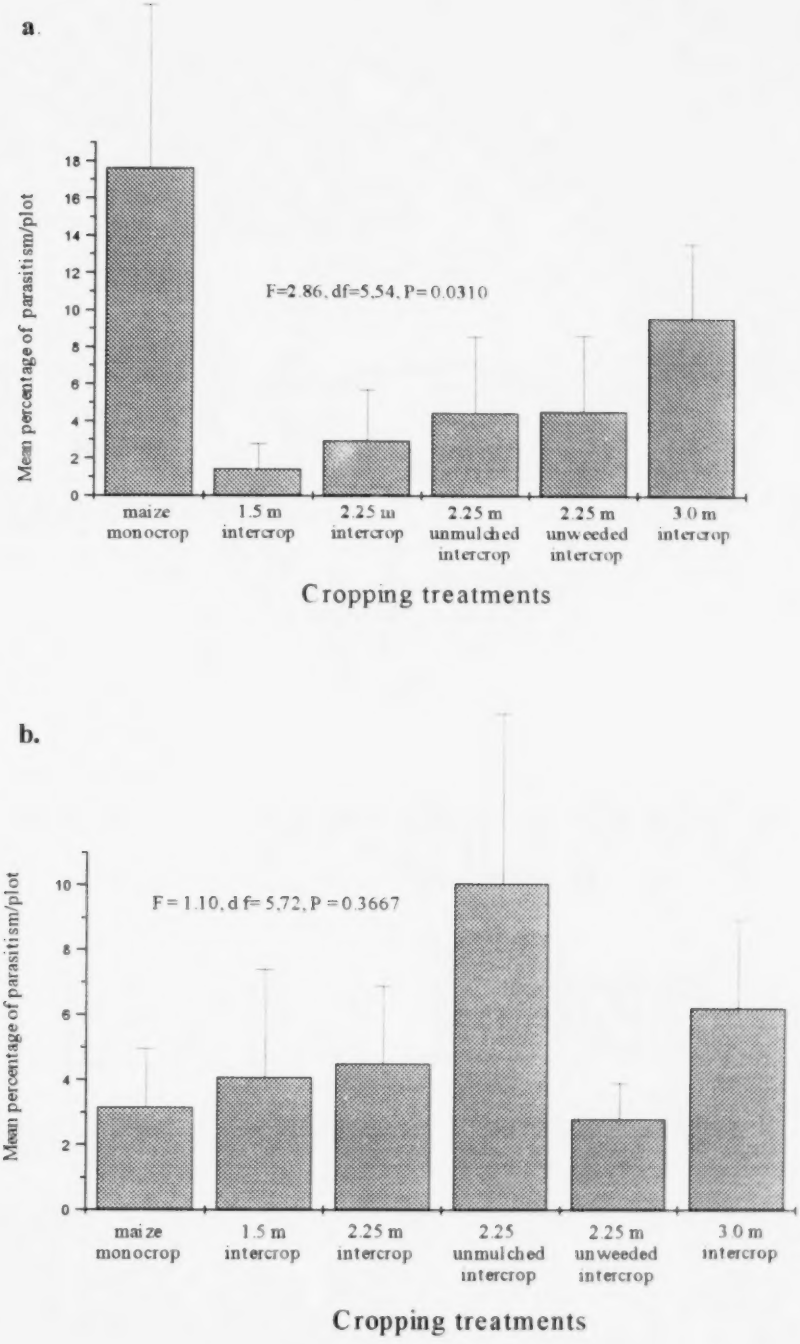


Figure 3.3: Average (±SE) percentage of stem borer larval and pupal parasitism per plot. Means represent treatment averages over cropping seasons. a. Mtwapa b. Amoyo

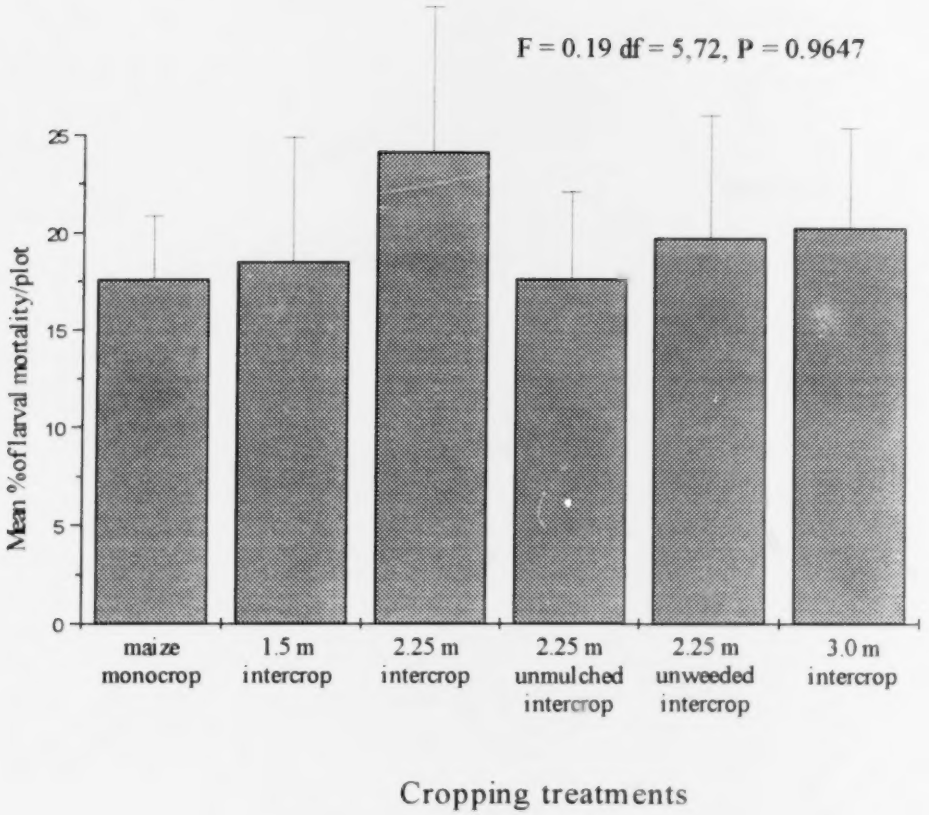


Figure 3.4: Average (±SE) percentage of stem borer larval mortality per plot at Mtwapa. Means represent treatment averages over cropping seasons.

Table 3.1: Orthogonal comparison for percentage of stem borer eggs parasitized per plot at Mtwapa

Contrasts	P
maize monocrop vs intercrops	0.32
weeded vs unweeded	0.76
mulched vs unmulched	0.08

Spacing regression analysis	R^2	P
linear	0.498	0.00
quadratic	0.032	0.38

Table 3.2: Orthogonal comparison for percentage of stem borer eggs depredated per plot at Mtwapa

Contrasts	P
maize monocrop vs intercrops	0.00
weeded vs unweeded	0.49
mulched vs unmulched	0.99

Spacing regression analysis	R^2	P
linear	0.060	0.39
quadratic	0.046	0.45

Table 3.3:Relative proportion (%) of stem borer larval and pupal parasitoids at Mtwapa and Amoyo

Parasitoid species	% borers parasitized	
	Mtwapa	Amoyo
Cotesia flavipes	3.09	15
Cotesia sesamiae	66.0	10
Cotesia rufricus	1.03	5
Cotesia sp.	1.03	35
Glyptapanteles africanus	nil	25
Apanteles sp	1.03	nil
Goniozus indicus	5.77	nil
Chelonus curvimaculatus	6.18	nil
Syzeuctus sp.	8.25	nil
*Pediobius furvus**	8.25	5
Aphanogmus sp **	nil	5
n=	356	125

* Pupal parasitoid

** Hyperparasitiod

Table 3.4: Orthogonal comparison for percentage of stem borer larval/pupal parasitism at Mtwapa and Amoyo

	Mtwapa	Amoyo
Contrasts	P	P
maize monocrop vs intercrops	0.40	0.00
weeded vs unweeded	0.16	0.85
mulched vs unmulched	0.13	0.77

Spacing regression analysis	R^2	P	R^2	P
linear	0.0135	0.67	0.471	0.01
quadratic	0.1237	0.21	0.065	0.03

Table 3.5: Orthogonal comparison for percentage of stem borer larval/pupal mortality at Mtwapa

Contrasts	P
maize monocrop vs intercrops	0.69
weeded vs unweeded	0.87
mulched vs unmulched	0.41

Spacing regression analysis	R^2	P
linear	0.018	0.64
quadratic	0.033	0.53

4. POPULATION DYNAMICS AND IMPACT OF THE LEUCAENA PSYLLID *HETEROPSYLLA CUBANA* Crawford (Homoptera: Psyllidae) IN THE MAIZE-LEUCAENA AGROFORESTRY SYSTEM

4.1 INTRODUCTION

The leucaena psyllid *Heteropsylla cubana* Crawford (Homoptera: Psyllidae), a native of Mexico, is a potentially serious pest of the widely used tropical leguminous tree species *Leucaena leucocephala* (Lam.) de Wit. The psyllid was first reported in Africa in 1991 from the Indian Ocean islands of Mauritius and Reunion (Hollis, 1992), and arrived in Kenya in July-August 1992 (Reynolds and Bimbuzi, 1992). It has since spread to most of eastern, central and southern Africa (Table 1.1).

The multivoltine psyllid has high potential for rapid population increase (Takara et al., 1990; Sutikno et al., 1991). It has a relatively short life cycle ranging from 10-21 days. Mean adult longevity is 10.6-14.5 days for females and 4.0-9.7 days for males. Eggs hatch in 2-3 days and there are 5 nymphal instars (Rauf et al., 1989; Parvathi et al., 1990; Takara et al., 1990). Females lay 211-241.4 eggs (Parvathi et al., 1990; Rauf et al., 1989). A mean production of 18.8 eggs per day (Takara et al., 1990), and a maximum of 60 eggs per day have been recorded (Rauf 1989). Like most pests with high rates of population growth, the psyllid is likely to become a serious pest in places it has invaded in the absence of its native natural enemies.

According to Napompeth (1994), both nymphs and adults of the psyllid feed by sucking sap on leucaena terminal shoots. Young flowers are also infested but less frequently. The older leaves are in most cases not attacked. Feeding may result in terminal shoots becoming desiccated and in stunted growth. High psyllid populations produce copious amounts of honeydew, giving rise to development of sticky black sooty mould

coating terminal shoots and leaflets. In case of heavy infestation, complete defoliation (through leaf fall) is common. Although plants recover in most cases, death of damaged plants has been known to occur.

Since this pest is new to tropical Africa and threatens the increasing use of leucaena for agroforestry in the region, there is need to seek inexpensive and yet effective and sustainable methods for its management. It was against this background that my studies aimed at evaluating the role and impact of the resource concentration hypothesis and the enemies hypothesis (see chapters 2 & 3 for reviews of these hypotheses) on the abundance of *H. cubana* in the maize-leucaena alley cropping system. Both these hypotheses predict some degree of protection from psyllid attack in the intercrop setting as compared to plots of pure leucaena. In addition, the study contributes to understanding of psyllid pest potential through monitoring the seasonal abundance and impact of the psyllid in relation to a representative group of natural enemies (Coccinelidae) and local climatic conditions.

4.2 MATERIALS AND METHODS

4.2.1 Study site, experimental design and plot-layout

Information about the study site, general experimental design and plot-layout have been given in Chapter 2. A summary is given here. The study was carried out at the Kenya Agricultural Research Institute (KARI) Regional Research Centre at Mtwapa, Coast Province (3°56' S, 39°44' E and 15m above sea level), and at the Kenya Forestry Research Institute experimental field site at Amoyo, Nyanza Province (0°10' S, 34°23 E and approximately 1400m above sea level). Both sites have a bimodal rainfall with a long cropping season from April to June, and an often unreliable short cropping season between October to December. Experimental plots were laid out in a randomized complete block design with five and four replications at Mtwapa and Amoyo respectively. Plots measured 18 x 12m at Mtwapa and 12x10m at Amoyo, separated by 6m buffer strips of bare ground. *Leucaena leucocephala* (Lam.) de Wit was planted in September 1992 in

hedgerows at a spacing of 0.5m within hedgerows. Six of the plots at Mtwapa were randomly assigned between row spacings of 1.5m, 1.5m, 2.25m, 2.25m, 2.25m and 3.0m, while at Amoyo, five plots were assigned between row spacings of 1.5m, 2.25m, 2.25m, 2.25m and 3.0m. During the cropping season, maize was planted between hedgerows at a spacing of 30cm within rows and 75cm between rows. 1, 2 and 3 rows of maize were planted between hedgerows planted 1.5m, 2.25m and 3m apart respectively. One of the 1.5m plots at Mtwapa was not planted to maize (leucaena monocrop). A seventh plot at Mtwapa and a sixth at Amoyo was planted to maize alone (maize monocrop). During maize planting, trees were cut back to 30cm above ground. Plots were mulched with leucaena foliage except for one of the 2.25m plots, and regularly weeded except for another of the 2.25m plots.

4.2.2 Abundance of psyllid nymphs and eggs

During the cropping seasons of long and short rains of 1993 and 1994 and during January to November 1995, starting 4 weeks after pruning of trees, ten leucaena plants were randomly selected from each plot. Psyllids were sampled using the method of Elder and Mayer (1990) with some modification. Shoot terminals consisting of one expanded and two unexpended leaves were carefully cut from each individual plant and individually placed in vials containing 70% alcohol. In the laboratory, the number of psyllid eggs and nymphs on each shoot terminal were counted under a dissecting microscope. Adults were not counted because they often jumped off when leaves were disturbed during sampling, leading to unreliable reflections of abundance. Data obtained werexpressed as number of psyllid nymphs or eggs per terminal shoot. Sampling was repeated every four weeks up to the next cropping season when leucaena plants were pruned. Psyllids were not sampled during the driest and hottest periods because terminal leaves required for the standard sample were not present.

4.2.3 Damage impacts of the psyllid

To obtain data about the impact of psyllid damage on leucaena, damage to each plot was rated monthly between the months of January to November 1995 using an empirical scale of 1 to 9 (Table 4.1). The rating was based on the general condition and health of leaves and stems and on an estimate of proportion of leaf loss due to psyllid damage. Overall damage rating for each month was calculated by averaging the rating of all plots for respective months.

Table 4.1: Psyllid damage rating scale

Rating	Damage symptom
1	No damage observed
2	Slight curling of leaves
3	Tips and leaves curling and yellowish
4	Tips and leaves severely curled and yellowish
5	Loss of up to 25% young leaves
6	Loss of 26% to 50% young leaves
7	Loss of 51% to 75% of young leaves
8	100% loss of young leaves and blackening of lower leaves
9	Blackened stem with no lower leaves

4.2.4 Abundance of predatory Coccinellidae

Ladybirds are generally known to be generalist predators of insects and have been reported to feed on psyllids (Naik et al., 1991; Mangoendihardjo et al., 1989b). Thus, I monitored their populations to obtain information about local predator abundance and activity. To do this, three rows of leucaena per plot were inspected visually for beetles at monthly intervals. Leucaena plants sampled were also counted. Beetles obtained were preserved in 70% alcohol, brought into the laboratory and counted. Data were expressed as number of ladybird beetles per plant. This sampling was conducted between June 1994 and November 1995, except in March and April when plants either had no leaves or were pruned.

4.2.5 Weather Data

Weather data for Mtwapa comprising mean monthly rainfall, temperature and relative humidity were obtained from the meteorological office of the Kenya Agricultural Research (KARI) Station at Mtwapa.

4.2.6 Data Analysis

Data collected were averaged for individual plots during each cropping season because of the unequal frequency of samples taken during the seasons, and analyzed by two-way (treatment x seasons) analysis of variance (ANOVA) (PROC GLM, SAS Institute, 1985). Both actual and arcsine transformed data met the assumptions of ANOVA and were analyzed. Thereafter, pre-planned orthogonal comparisons were made to test for effects of intercropping, weeds and mulch. Regression analysis (PROC REG, SAS Institute, 1985) was used to test for linear and quadratic relationships of spacing on abundance of psyllids and ladybird beetles. However at Amoyo, comparisons for effects of intercropping *per se* could not be made because there were no leucaena monoculture plots. Overall population patterns of psyllids over time was performed by plotting data collected during each month/ trapping period.

4.3 RESULTS

4.3.1 Psyllid abundance

4.3.1.1 Effects of sites and treatments

Psyllids were much more abundant on the coast at Mtwapa than in the highlands at Amoyo. The seasonal mean number of psyllid nymphs per plant ranged from 30.0 ± 3.57 to 35.4 ± 3.89 among treatments at Mtwapa and 6.2 ± 1.87 to 8.7 ± 2.90 at Amoyo (Figures 4.1a & b respectively). Similarly, estimates for eggs ranged from 33.8 ± 5.9 to 49.9 ± 10.76 at Mtwapa and 6.7 ± 1.67 to 11.1 ± 3.03 at Amoyo (Figures 4.2a & b respectively). Differences among treatments were not statistically significant for either nymphs or eggs (Tables 4.2 and 4.3 respectively). However, at Mtwapa, there was significant linear relationship between spacing and number of eggs (Table 4.3), suggesting that psyllid oviposition became more concentrated with increasing hedgerow spacing. Apart from the effect of spacing on abundance of eggs, vegetation structure had no consistent effect on the abundance of psyllid nymphs and eggs.

4.3.1.2 Seasonal patterns

Abundance of psyllid nymphs at Mtwapa dropped to lowest numbers during months with very little or no rain, and during seasons with heavy rainfall. Immediately after periods of rainfall, when soil moisture allowed rapid plant growth, nymphal abundance rose rapidly and remained high, as long as subsequent rainfall was moderate (Figure 4.3a). There was no clear pattern of abundance of nymphs in relation to relative humidity or temperature (Figures 4.3b & c respectively).

Although detailed weather data for Amoyo was not available, pattern of nymphal abundance (Figure 4.4) was similar to that of Mtwapa, showing a striking relationship with rains. However, psyllid populations were generally much lower than at Mtwapa, with very few to virtually no psyllids during the dry spells and at peak rainy season.

The effect of environmental parameters on psyllid reproduction as reflected by abundance of psyllid eggs, was similar to that of nymphs. Rainfall had a marked effect on abundance of eggs, with few to no eggs observed during the dry season and periods of heavy rainfall (Figure 4.5a). Abundance of eggs peaked sharply soon after peak rains as rainfall amounts fell to more moderate levels. Egg numbers gradually fell soon after, as the rainy season ended. Response of egg abundance to both relative humidity and temperature also showed no definite pattern (Figures 4.5b & c respectively).

4.3.2 Damage and impacts of psyllids

Damage to leucaena foliage at Mtwapa increased progressively from January and reached its peak in April when plants had no leaves, stems were blackened and twigs looked dry (Table 4.5). There was new growth of shoots in May with terminal shoot/leaves categorized as healthy to slightly curled. Soon after, damage intensity rapidly increased and reached another peak in July. At Amoyo however, foliar damage was comparatively low, with plants looking much healthier and hardly ever losing their leaves at any time of the year (Table 4.5).

When damage rating was superimposed on weather data (Figure 4.6a), it was evident that damage increased with decreasing rainfall. Damage to foliage tended to be cumulative as there was a progressive increase in damage observed during the prolonged dry season from January to April. When damage was related to psyllid populations (Figure 4.6b), it was usually higher long after psyllid populations had peaked and were much lower (except in July). I conclude that psyllid populations were dependent upon the availability of suitable terminal shoots, and that damage to foliage was as a result of the cumulative and interactive effect of both psyllids and moisture availability.

4.3.3. Ladybird beetle abundance

Although conspicuous ladybird adults were relatively rare on leucaena, the average number of ladybird beetles at Mtwapa ranged from 0.035 to 0.048/plant among treatments (Figure 4.7). Statistical analysis of data showed that differences among treatments were not significant (Table 4.4), indicating that vegetation structure had no influence on the abundance of ladybirds.

Seasonal populations of ladybirds appeared to follow the population pattern of psyllids. Beetle abundance rose in response to rising psyllid numbers and vice versa (Figure 4.8). The response appeared to be more strongly linked to nymphal abundance than to that of eggs, suggesting some evidence that the beetles responded to presence of psyllids.

4.4 DISCUSSION AND CONCLUSIONS

4.4.1 Abundance of psyllid nymphs and eggs and ladybird beetles within the maize-leucaena agroforestry system

Vegetation structure had no apparent effect on the abundance of psyllid nymphs and eggs. Thus, the central predictions of the resource concentration hypothesis, i.e., that non-host species disrupt the ability of a pest to attack its proper host efficiently, was not supported. Moreover, the significant increase in number of eggs with increase in spacing observed at Mtwapa not only contradicts the hypothesis, but also shows the variability of herbivore response to resource concentration. These results are not unusual. Reviews of the resource concentration hypothesis revealed that 56% of herbivores had lower population densities, 16% had higher, and 28% showed no difference in polycultures when compared to monocultures (Andow, 1986, 1988), suggesting that diversity does not always lead to reduction in pest numbers.

One mechanistic basis of the resource concentration is that herbivores are less likely to locate their host plant efficiently in diverse habitats because of the masking and dilution of the attractant stimuli by non-host plants. These attractants are in the form of volatile plant chemicals which play a major role in host searching and selection by adult insects (Dethier, 1980, 1982; Metcalf, 1986; Saxena, 1987; Tingle et al., 1990). The leucaena psyllid *Heteropsylla cubana* uses host-plant odour in its host-plant preference orientation behaviour (Lapis and Borden, 1993), and therefore I expected that the psyllids would be less likely to locate their host plants in the intercropping situation. However, this prediction failed, probably because of the mode of dispersal and spread of psyllids which, because of their relatively small size and poor flight ability (common name 'jumping plant lice'), appears to be largely wind assisted. Thus, the effect of non-host plants on host searching and selection, which require active and controlled flight by the herbivore, may be relatively minor.

A second component of the resource concentration hypothesis is that non-hosts act as mechanical barriers by blocking the dispersal of herbivores across the polyculture. However, in my studies, leucaena plants were always present during the non-cropping season when there was no maize to reduce dispersal. This may have led to more or less equal distribution of psyllids among treatment plots. Furthermore, spacing of leucaena plants within rows and even between the 1.5m hedgerows was close enough to allow contact between neighboring plants. Under this kind of situation, psyllids could easily spread by crawling from one plant to another, diminishing any blocking effect of non-host intercrops. Therefore, future studies should explore spacing patterns that ensure complete isolation or non-contact between host plants.

Psyllid populations were generally much higher at Mtwapa than at Amoyo. My data are insufficient to explain this, although the lack of notable population growth at Amoyo during the period of my study suggests that the differences do not simply reflect more recent establishment there. I suggest that site-specific studies be conducted to determine the biotic and abiotic factors involved in the regulation of psyllid populations. Such information will be useful in making recommendations about the suitability of

leucaena for specific sites and, perhaps ultimately for designing pest management strategies for the psyllid.

The number of ladybird beetles at Mtwapa did not differ significantly between treatments indicating that vegetation structure had no influence on the abundance of the generalist predatory ladybird beetles. Thus, Root's (1973) enemies hypothesis that natural enemies will be more abundant in polycultures than in monocultures was not supported with respect to this taxon despite the fact that ladybirds appear to respond to changes in psyllid density. However, a review of the enemies hypothesis reported that 13.2% did not show any difference between polycultures and monocultures (Andow, 1991). The enemies hypothesis may better explain population level responses of generalist than specialist enemies because the provision of alternative food and microhabitats associated with diverse vegetation are more relevant to enemies with broad feeding ranges than to specialist enemies (Sheehan, 1986; Russell, 1989). My results for the generalist ladybirds are therefore conspicuously inconsistent with those that have supported the enemies hypothesis. I conclude that crop diversity does not always lead to reduction in pest numbers or increased natural enemy abundance, and that resource concentration and positive effects on natural enemy populations do not invariably provide benefits under agroforestry systems.

4.4.2 Seasonal abundance of leucaena psyllid and ladybird beetles

Abundance of psyllid nymphs and eggs were lower during the extreme dry and extreme wet seasons. Their numbers increased soon after the onset of rains, but only significantly after peak rainy seasons, with populations peaking after rains had declined considerably. Few psyllids were recorded, particularly at Amoyo, during the extended dry season (February-April) and peak rainy season (May). Several studies have similarly reported higher adult and nymphal populations when rainfall was low and during the dry season, while lower populations of the leucaena psyllid were observed during the rainy season, particularly when rainfall was heavy (Escalada, 1989; Mangoendihardjo et al.,

1989a; Villacarlos et al., 1989). In addition, psyllid populations declined with extreme high temperatures and low relative humidity (Naik et al., 1991, Napompeth, 1994). Though there was no definite relationship between psyllid abundance and either temperature and relative humidity in my studies, in the tropics both climatic parameters are largely dependent on the rainfall pattern, which had a clear effect on psyllid populations.

Villacarlos et al. (1989) suggested that high moisture resulted in epizootics of entomogenous pathogens and caused a decrease in psyllid populations. The effect of pathogens, though not considered in my studies, could be an important mortality factor, particularly at the often highly humid coastal strip of Kenya. However, my study provides no evidence for this conjecture.

Psyllid population build-up was in response to growth of new tender shoots following seasonal rainfall and periodic cultural treatment of pruning. However, even in the presence of suitable habitable shoots, psyllid populations remained low when there was continuous heavy rainfall, probably from insects being washed away, as suggested by Escalada (1989). Conversely, the extended dry season together with low relative humidity and high temperatures caused decreased vegetative growth leading to reduced or lowered carrying capacity of plants, and therefore to low insect populations.

Populations of ladybird bird beetles appeared to be influenced by those of their prey, particularly nymphs, and responded little to egg abundance patterns. Similar results were obtained by Naik et al. (1991) who reported an increasing incidence of natural enemies in response to increasing psyllid populations in India, and that psyllid populations were reduced by the predatory effects of ladybird beetles, including the exotic *Curinus coerulus*, which was released against the psyllid. However, in my studies, ladybird populations were relatively very low, and the just over half a dozen species encountered did not appear to have any noticeable impact on the psyllids. Similar observations were made on the endemic natural enemies of the leucaena psyllid in Indonesia where the predatory Coccinellids *Coccinella arcuata* and *Coccinella repanda* had very low predation capacity for psyllids (Mangoendihardjo et al., 1989b).

4.4.3 Damage impacts of psyllid

Damage to foliage was as a result of the cumulative and interactive effect of both the feeding effect of psyllids and prevailing environmental/climatic conditions, and did not reflect the actual population of and/or damage by psyllids at a given time. Very little damage was observed on young shoots/leaves that sprouted from freshly pruned plants at the beginning of the rainy season when psyllid populations were generally low. Similarly, damage to foliage was much less during periods of heavy rainfall. However, as the season progressed and less rain was received, psyllid populations grew and the damage ratings reached their peaks. Similar results were reported by Wheeler and Brewbaker (1989) who, using a 1-10 damage rating, obtained greater damage during low or limiting rainfall. Since climatic conditions at Amoyo is categorized as being of the semi-arid to semi-humid type (Sombroek et al., 1982), the relatively greater damage done to plants at Mtwapa than at Amoyo could be largely attributed to the higher psyllid populations in the former site, and not to more rainfall at the latter.

4.4.4 Conclusions

These studies show that alley cropping leucaena with maize had no effect on the abundance of the leucaena psyllid *Heteropsylla cubana* or its coccinellid predators. Therefore, neither the resource concentration hypothesis nor the enemies hypothesis corroborated for leucaena in this system. Psyllid populations were influenced by weather (mainly rainfall) and availability of suitable shoots. New growth of young shoots following rainfall encouraged psyllid abundance as long as weather conditions were not extreme. Though populations of the generalist ladybird beetles followed that of its psyllid prey, they did not appear to have significant effect on prey populations. Observed damage on leucaena based on the visual scale represented the cumulative and interactive effect of both the feeding activity of psyllids and prevailing environmental/climatic conditions, and not the actual population of and/or damage by psyllids at a given time.

Field life table studies will be necessary to determine fully the role of both biotic and abiotic factors on psyllid populations, and establish the major differences in population regulation between sites, like those observed at Amoyo and Mtwapa. This will allow us to make predictions about psyllid populations and subsequent plant damage upon which we could base site-specific recommendations about use and adoption of leucaena as an agroforestry tree species. Further work is required to develop a pest management strategy against the psyllid.

4.5 REFERENCES

Andow, D. A. 1986. Plant diversification and insect population control in agroecosystems, pp. 277-386. *In.* D. Pimentel [ed.], Some aspects of integrated pest management. Dept. Entomology, Cornell University, Ithaca, NY.

Andow, D. A. 1988. Management of weeds for insect manipulation in agroecosystems, pp.265-301. *In* M. A. Altieri & M. Liebman [eds.], Weed management in agroecosystems: ecological approaches. CRC, Boca Raton, Fla.

Andow, D. A. 1991. Yield loss to arthropods in diverse agroecosystems. Environ. Entomol. 10: 1228 - 1235.

Dethier, V. G. 1980. Evolution of receptor sensitivity to secondary plant substances with special reference to deterrents. Am. Nat. 115: 45-66.

Dethier, V. G. 1982. Mechanisms of host plant recognition. Entomol. Exp. Appl. 31:49-56.

Elder, R. J. and D. G. Mayer. 1990. An improved sampling method for *Heteropsylla cubana* Crawford (Homoptera: Psyllidae) on *Leucaena leucocephala*. J. Aust. ent. Soc. 29: 131-137.

Escalada, R. G. 1989. Leucaena psyllid trial in the Philippines. Leucaena Research Reports 10: 3-7

Hollis, D. 1992. Leucaena psyllid, *Heteropsylla cubana* Crawford newly recorded in Mauritius and Reunion. FAO Plant Protection Bulletin 40 (1-2): 49 - 50.

Lapis, E. B. and J. H. Borden. 1993. Olfactory discrimination by *Heteropsylla cubana* (Homoptera: Psyllidae) between susceptible and resistant species of *Leucaena* (Leguminosae). J. Chem. Ecol. 19: 83 -90

Mangoendihardjo, S., F. X. Wagiman., Y. A. Trisyono and M. Sudjono. 1989a. Seasonal abundance of leucaena psyllid populations in Yogykarta, Indonesia. *In* B. Napompeth and K. G. MackDicken (eds.), Leucaena Psyllid: Problems and Management. Proceedings of a Workshop, January 16-21, Winrock International/IDRC/NFTA, Bogor, Indonesia. pp. 111-113.

Mangoendihardjo, E. Mahrub and J. Warrow. 1989b. Endemic natural enemies of the leucaena psyllid in Indonesia. *In* B. Napompeth and K. G. MackDicken (eds.), Leucaena Psyllid: Problems and Management. Proceedings of a Workshop, January 16-21, Winrock International/IDRC/NFTA, Bogor, Indonesia. pp. 159-161.

Metcalf, R. L. 1986. Plant volatiles as insect attractants. Crit. Rev. Plant Sci. 5: 251-301.

Naik, S., Rajagopal, D. and M. K. Munegowda. 1991. Population dynamics of the subabul psyllid *Heteropsylla cubana* Crawford (Homoptera: Psyllidae) and its interaction with natural enemies. Leucaena Research Reports 12: 49-52.

Napompeth, B. 1994. Leucaena psyllid in the Asia Pacific region: Implications for its management in Africa. RAPA-FAO publication 1994/13.

Parvathi, C., V. V. Belavadi and G. Thimmaiah. 1990. Biology of the leucaena psyllid *Heteropsylla cubana* Crawford (Homoptera: Psyllidae) in south India. Indian Journal of Forestry 13: 154-157.

Rauf, A., P. Hidayat., N. Maryana and I. W. Winasa. 1989. Biology and demography of *Heteropsylla cubana* Crawford (Homoptera: Psyllidae). *In* B. Napompeth and K. G. MackDicken (eds.), Leucaena Psyllid: Problems and Management. Proceedings of a Workshop, January 16-21, Winrock International/IDRC/NFTA, Bogor, Indonesia. pp. 114 - 117.

Reynolds, L. and S. Bimbuzi. 1992. Leucaena psyllid arrives in Kenya. Agroforestry today, 4(3): 2.

Root, R. B. 1973. Organization of plant - arthropod association in simple and diverse habitats: The fauna of collards (*Brassicae olevaceae*). Ecol . Monogr. 43: 95-124.

Russell, E. P. 1989. Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. Environ. Entomol. 18: 590-599.

Statistical Analysis Systems Institute Inc. 1985 SAS Users Guide. Statistics, Version 5 edn. SAS Institute Inc., Cary, NC.

Saxena, K. N. 1987. Ovipositional responses of *Chilo partellus* to certain sorghum cultivars in relation to their resistance or susceptibility to the stem borer. Proc. 6th internat. symp. Insect-Plant relationships. D. W. Junk Publishers, Dordrecht, pp. 313-318.

Sheehan, W. 1986. Response by specialist and generalist natural enemies to agroecosystem diversification: a selective review. Environ. Entomol. 15: 456-461.

Sombroek, W. G., H. M. H. Braun and B. J. A. Van Der Pouw. 1982. Exploratory soil map and agroclimatic zone map of Kenya. Kenya Soil Survey, Nairobi.

Sutikno, A. I, J. Darma and H. P. B. P. Ternak. 1991. Mimosine content in the sap of *Leucaena* species resistant and susceptible to *Heteropsylla cubana* Crawford. Toxicological and Environmental Chemistry 33: 79 - 83.

Takara, J. M., R. J. Dinker, W. T. Nagamine and K. K. Teramoto. 1990. Biology and reproductive rate of the leucaena psyllid *Heteropsylla cubana* Crawford. Proc. Hawaii. Entomol. Soc. 30: 23 - 30

Tingle, F. C., E. R. Mitchell and R. R. Heath. 1990. Preference of mated *Heliothis viriscens* and *H. subflexa* females for host and nonhost volatiles in a flight tunnel. J. Chem. Ecol. 16:2889-2898.

Villacarlos, L. T., R. V. Paglinawan and R. P. Robin. 1989. Factors affecting leucaena psyllid populations in Leyte, Philippines. *In* B. Napompeth and K. G. MackDicken (eds.), Leucaena Psyllid: Problems and Management. Proceedings of a Workshop, January 16-21, Winrock International/IDRC/NFTA, Bogor, Indonesia. pp. 122-127.

Wheeler, R. A. and J. L. Brewbaker (1989) Leucaena Research Reports 10: 11-15

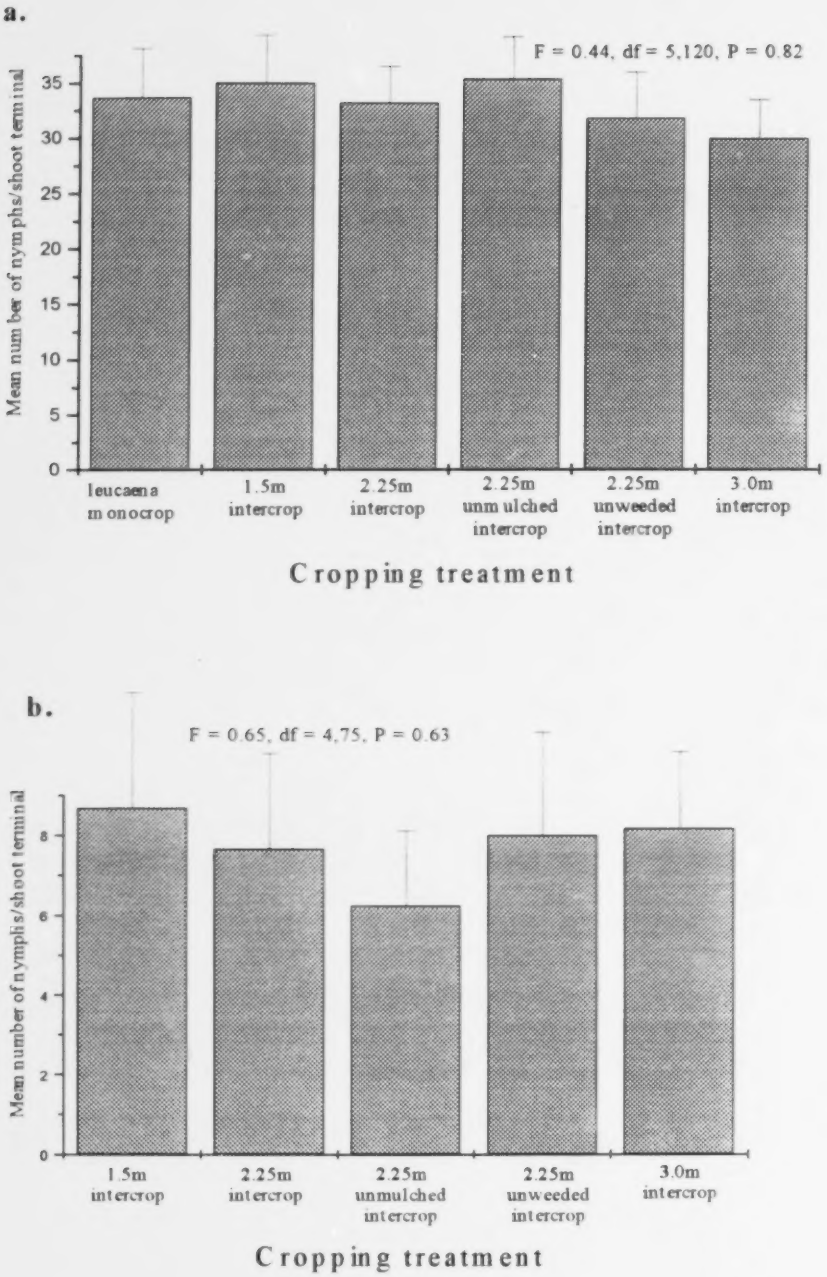


Figure 4.1: Average (±SE) number of psyllid nymphs/shoot terminal. Means represent treatment averages over four cropping seasons. a. Mtwapa b. Amoyo

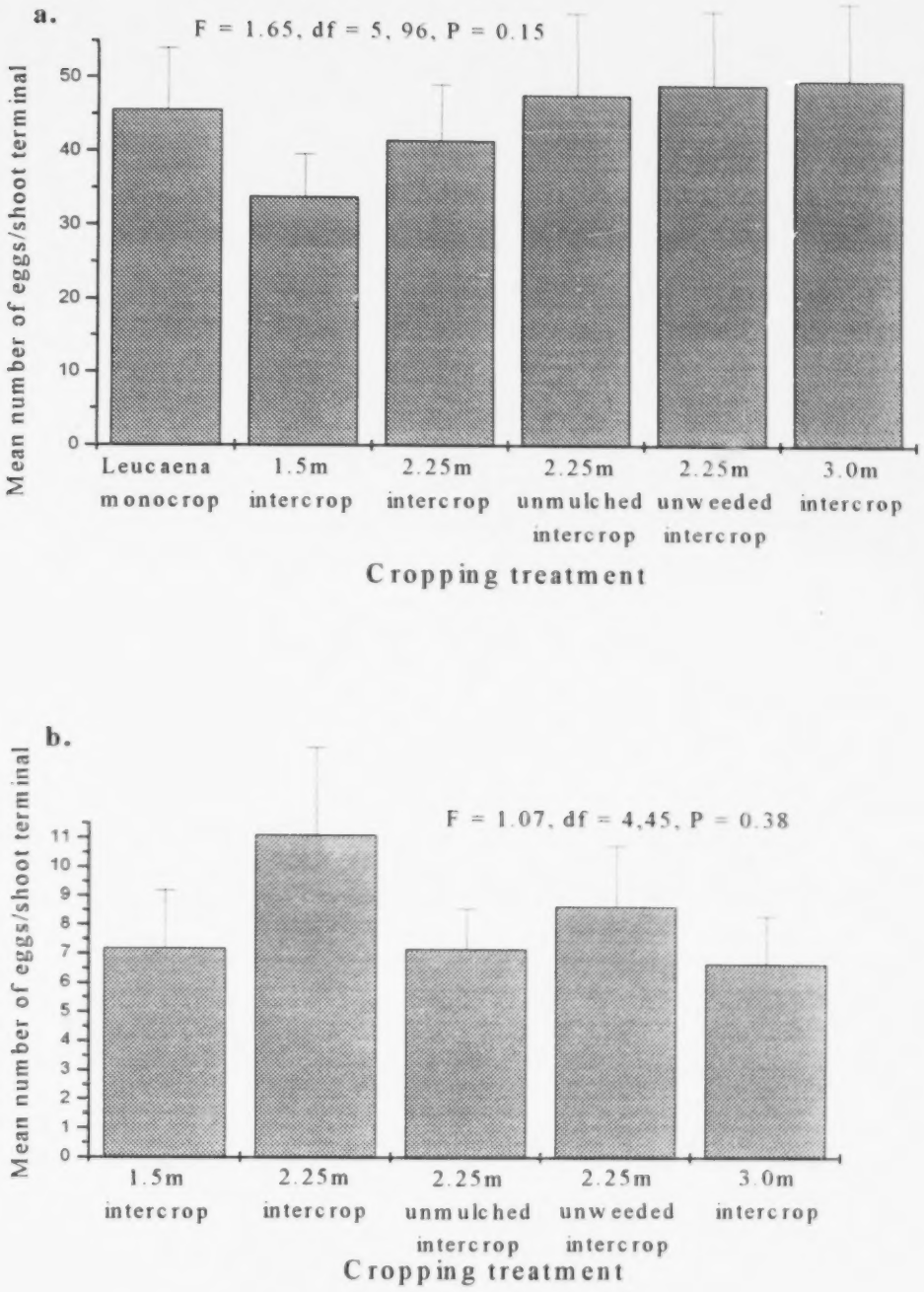


Figure 4.2: Average (±SE) number of psyllid eggs/shoot terminal. Means represent treatment averages over four cropping seasons. a. Mtwapa b. Amoyo

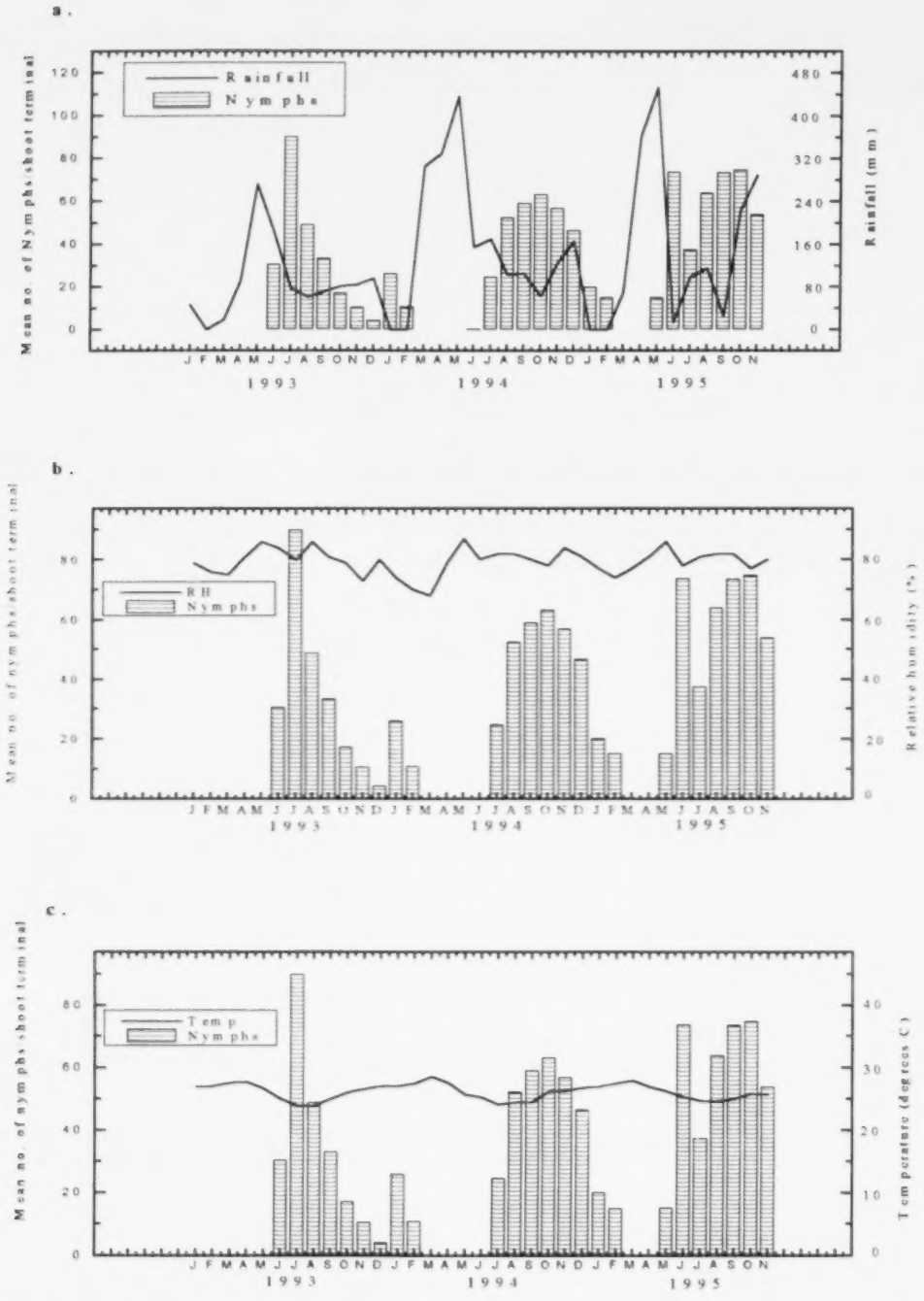

a.
Rainfall
Nymphs
Mean no. of Nymphs shoot terminal
Rainfall (mm)
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N
1993
1994
1995
b.
RH
Nymphs
Mean no. of nymphs shoot terminal
Relative humidity (%)
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N
1993
1994
1995
c.
Temp
Nymphs
Mean no. of nymphs shoot terminal
Temperature (degrees C)
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N
1993
1994
1995

Figure 4.3: Seasonal abundance of psyllid nymphs in relation to climatic conditions at Mtwapa Means represent averages for pooled data per sampling period during each month. a. temperature, b. relative humidity, c. temperature.

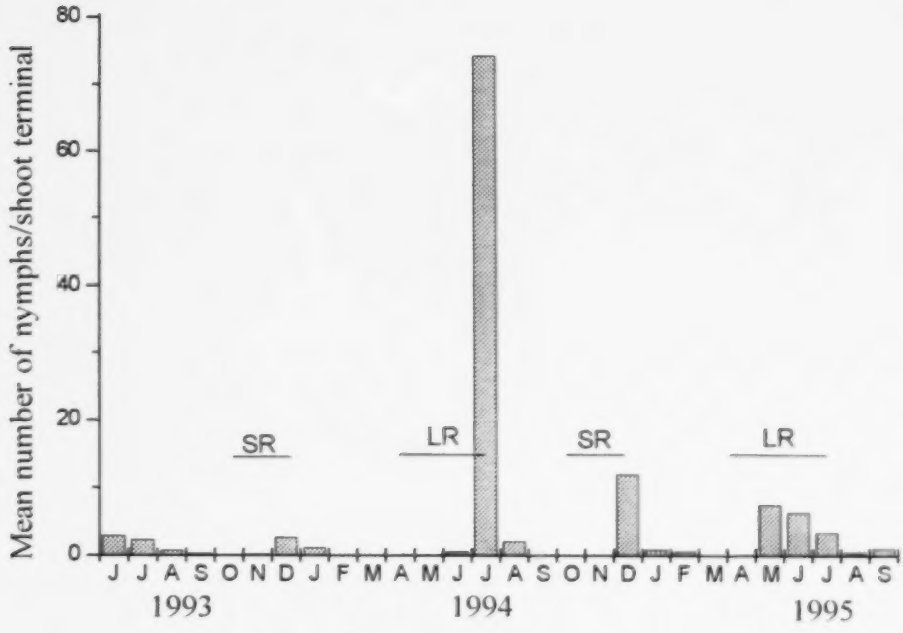


Figure 4.4: Seasonal abundance of psyllid nymphs at Amoyo. Means represent averages for pooled data per sampling period during each month. LR: Long rains SR: Short rains

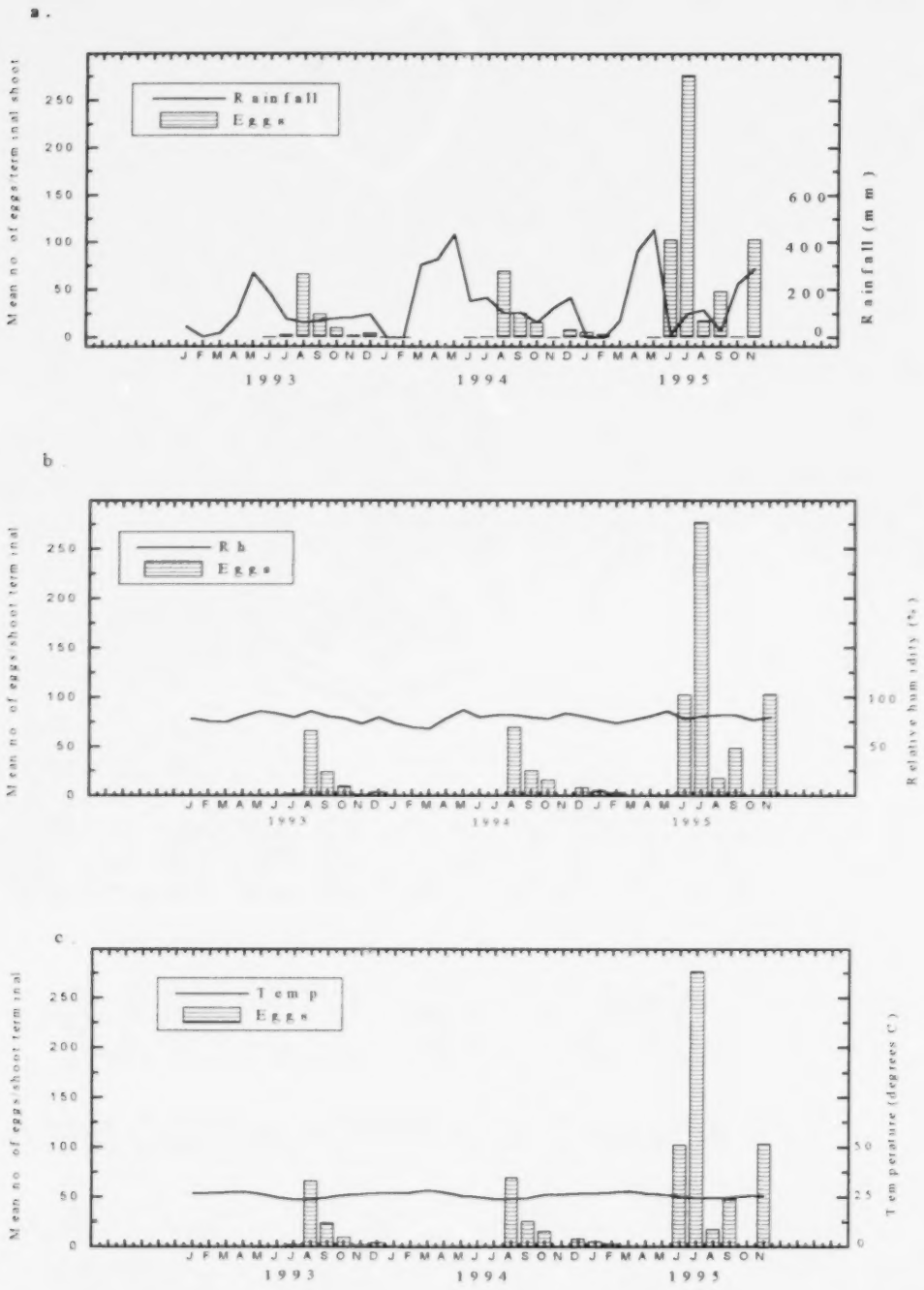


Figure 4.5: Seasonal abundance of psyllid eggs in relation to climatic conditions at Mtwapa. Means represent averages for pooled data per sampling period during each month. a. temperature, b. relative humidity, c. temperature.

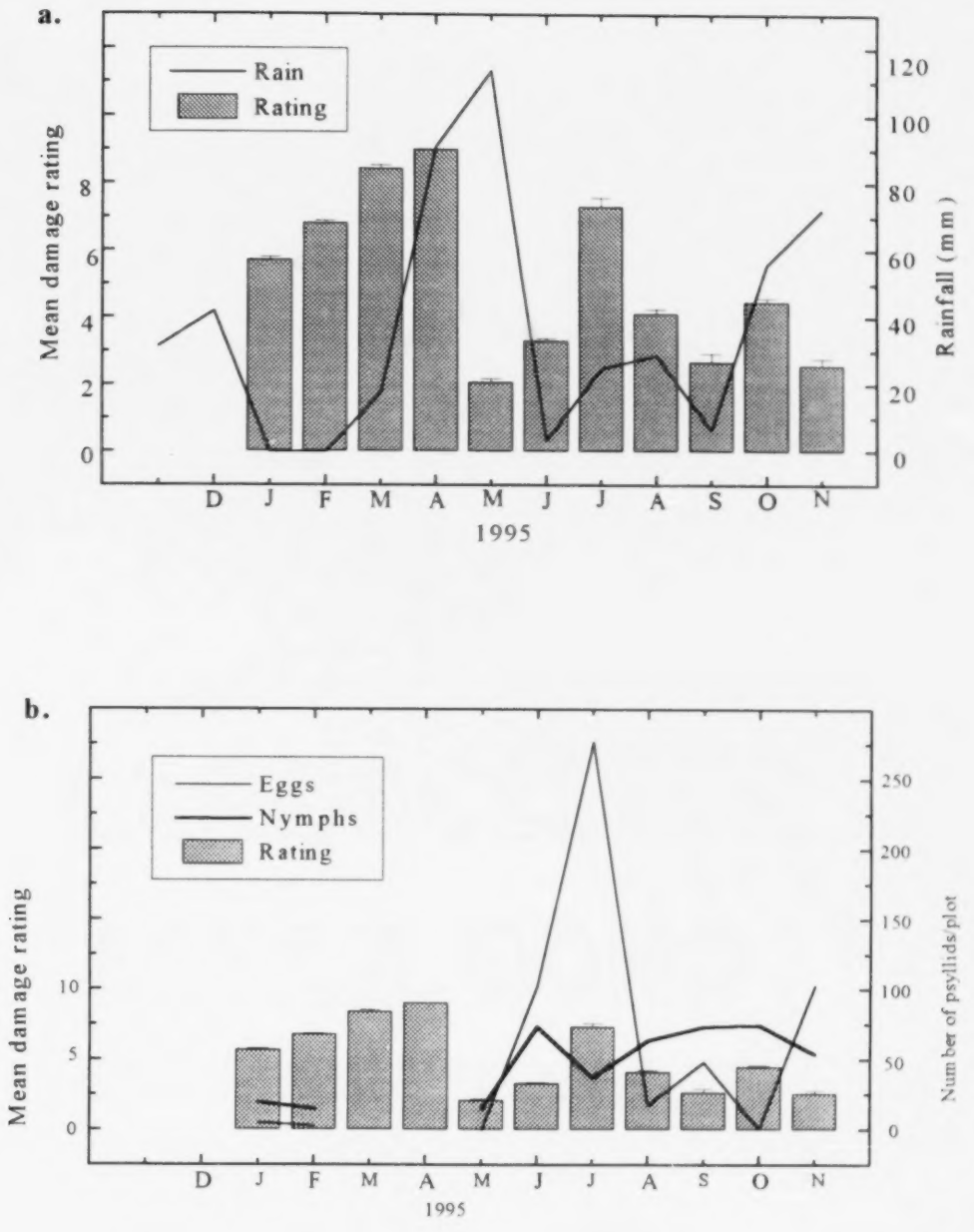


Figure 4.6: Average (±SE) damage rating of leucaena in relation to rainfall and psyllid abundance at Mtwapa. Means represent averages for pooled data per sampling period during each month. a. rainfall, b. psyllid abundance.

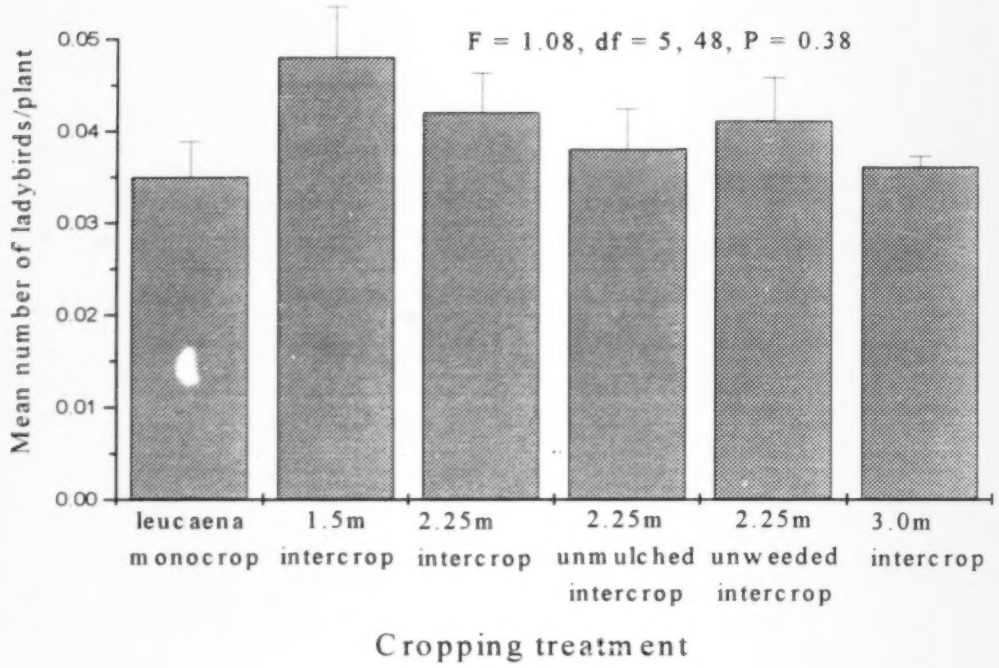


Figure 4.7: Average (±SE) number of ladybird beetles per plant at Mtwapa. Means represent treatment averages over two cropping seasons.

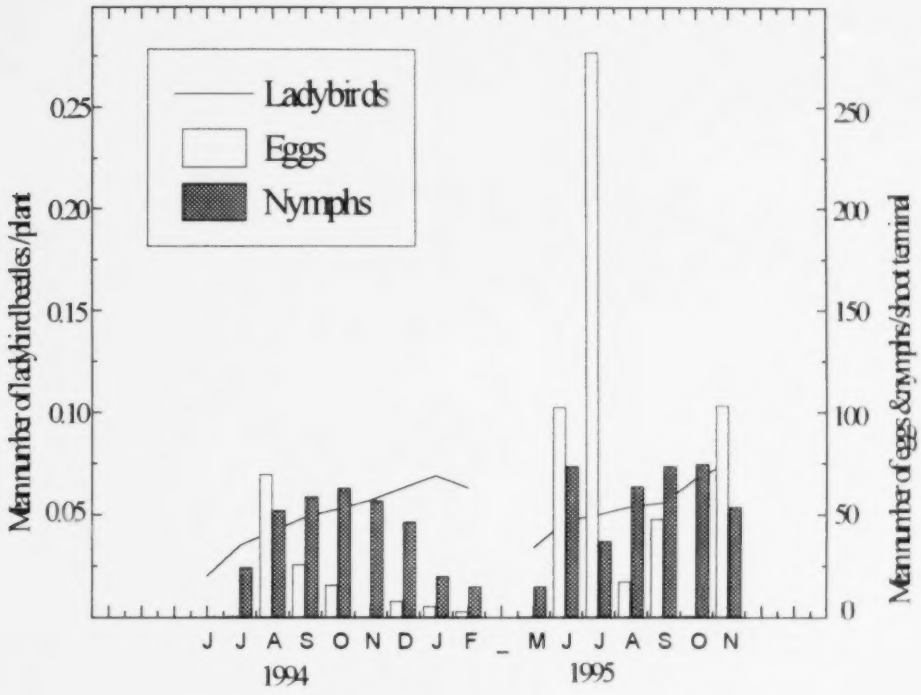


Figure 4.8: Seasonal abundance of ladybird beetles in relation to psyllid populations at Mtwapa. Means represent averages for pooled data per sampling period during each month.

Table 4.2: Orthogonal comparisons for mean number of psyllid nymphs per shoot terminal at Mtwapa and Amoyo

	Mtwapa		Amoyo	
Contrasts		P		P
leucaena monocrop vs intercrops		0.86		
weeded vs unweeded		0.51		0.46
mulched vs unmulched		0.62		0.38
Spacing regression analysis	R^2	P	R^2	P
linear	0.117	0.23	0.014	0.72
quadratic	0.004	0.82	0.043	0.54

Table 4.3: Orthogonal comparisons for mean number of psyllid eggs per shoot terminal at Mtwapa and Amoyo

	Mtwapa		Amoyo	
Contrasts		P		P
leucaena monocrop vs intercrops		0.83		
weeded vs unweeded		0.43		0.82
mulched vs unmulched		0.35		0.12
Spacing regression analysis	R^2	P	R^2	P
linear	0.305	0.04	0.002	0.88
quadratic	0.000	0.95	0.183	0.19

Table 4.4: Orthogonal comparisons for mean number of ladybird beetles per plant at Mtwapa

Contrasts	P
leucaena monocrop vs intercrops	0.27
weeded vs unweeded	0.77
mulched vs unmulched	0.55

Spacing regression analysis	R^2	P
linear	0.204	0.11
quadratic	0.001	0.93

Table 4.5: Leucaena damage rating for Mtwapa and Amoyo (1995)

Month (1995)	Mean damage rating	
	Mtwapa	Amoyo
January	5.7	1
February	6.8	1.22
March	8.43	1.36
April	9	2.54
May	2.07	3.85
June	3.3	1.25
July	7.3	1.4
August	2.67	1
September	4.1	1
October	2.57	*
November	4.47	*

* = not rated

5. GROUND-DWELLING BEETLES AND SPIDERS IN THE MAIZE-LEUCAENA AGROFORESTRY SYSTEM

5.1 INTRODUCTION

Epigaeic arthropods have received much attention in agroecosystems because they are numerically dominant, exist in diverse assemblages and play important ecological roles (Potts and Vickerman, 1974; Thiele, 1977; Luff, 1987; Winder, 1990; Cárcamo and Spence, 1994). Ground beetles (Carabidae) for example, together with other predatory arthropods (i.e. spiders), are capable of reducing pest populations significantly, and provide significant natural resistance to pest outbreaks in cultivated crops (Best and Beegle, 1977; Purvis and Curry, 1984; Brust et al., 1986). Although herbivorous species may be pests of cultivated crops, some may partly control weed populations through seed consumption (Lund and Turpin, 1977). Others are detritivorous and are involved in nutrient recycling (Robertson et al., 1994). Consequently, there is interest in conserving and enhancing populations of beneficial ground-dwelling predatory arthropods as a pest management alternative to insecticides (Cárcamo and Spence, 1994; Robertson et al., 1994) as a component of low-input crop production technologies that aim to increase the ecological sustainability of agroecosystems. Such technology is crucial to resource-limited farmers particularly in tropical Africa, who cannot afford expensive agrochemicals for pest control.

One theme in sustainable agriculture relies on increasing vegetational diversity as a general approach of increasing system stability. Intercropping and agroforestry are polycultural systems that promote vegetational diversity, and these have been frequently proposed to promote abundance and diversity of generalist natural enemies (Root, 1973; Risch, 1981; Andow and Risch, 1985; Sheehan, 1986), and at the same time, reduce abundance of herbivorous species (Root, 1973; Risch 1980, 1981; Risch et al., 1983; Andow, 1983a, b, 1986, 1988). The mechanisms involved in reducing pest problems in these systems have been explained by two general hypotheses: the enemies hypothesis and

the resource concentration hypothesis. The enemies hypothesis posits that vegetational diversity increases population size and impacts of entomophagous natural enemies that regulate populations of herbivorous arthropod pests (Risch et al., 1983; Herzog and Funderburk, 1986; Russel; 1989, Andow, 1991). On the other hand, the resource concentration hypothesis which largely applies to specialist herbivores, suggests that that non-host species disrupt the ability of a pest to attack its proper host efficiently (Vandermeer, 1990). In addition to the potential favourable effects in relation to insect pests, vegetationally diverse systems are more likely to retain a broad mix of species and may therefore have broad conservation implications for landscapes increasingly dominated by agriculture.

The effects of multiple cropping on ground-dwelling arthropod populations have been studied largely using temperate ground beetles (e.g. Brust et al., 1986; Perfecto et al., 1986; Cárcamo and Spence, 1994). Comparable studies are lacking for tropical polycultural systems especially in an agroforestry context. My study examined the impact of the maize-leucaena agroforestry system on the abundance of ground-dwelling beetles and spiders in coastal Kenya. Based on the two general hypotheses, it was expected that there would be greater abundance of spiders, predatory and detritovorous beetles, but fewer herbivorous beetles in the intercrops than in the monocrops.

5.2 MATERIALS AND METHODS

5.2.1 Study site, experimental design and plot-layout

Information about the study site, general experimental design and plot-layout have been given in Chapter 2. A brief summary is given here. The study was carried out at the Kenya Agricultural Research Institute (KARI) Regional Research Centre at Mtwapa, Coast Province, Kenya (3°56' S, 39°44' E and 15m above sea level). The coastal strip has a long cropping season from April to June, and an often unreliable short cropping season between October to December. Experimental plots were laid out in a randomized

complete block design with five replications. Plots measured 18 x 12m separated by 6m buffer strips of bare ground. *Leucaena leucocephala* (Lam.) de Wit was planted in September 1992 in hedgerows at a spacing of 0.5m within hedgerows. Six of the plots were randomly assigned between row spacings of 1.5m, 1.5m, 2.25m, 2.25m, 2.25m and 3.0m. During the cropping season, maize was planted between hedgerows at a spacing of 30cm within rows and 75cm between rows. 1, 2 and 3 rows of maize were planted between hedgerows planted 1.5m, 2.25m and 3m apart respectively. One of the 1.5m plots was not planted to maize (leucaena monocrop) while a seventh plot was planted to maize alone (maize monocrop). During maize planting, trees were cut back to 30cm above ground. Plots were mulched with leucaena leaves except for one of the 2.25m plots, and regularly weeded except for another of the 2.25m plots.

5.2.2 Sampling of ground-dwelling beetles and spiders

Pitfall traps were used to sample ground-dwelling beetles and spiders during the cropping seasons associated with the long and short rains of 1993 and 1994. Traps consisted of 500ml plastic jars, two of which were buried along the centre line of each plot, each 6m from either plot edge and 6m apart. Each jar was half filled with 10% formaldehyde solution to prevent decomposition of soft bodied animals, and a little liquid soap added to reduce surface tension. A plastic dish (25cm diameter) was suspended on metal rods 7 cm above each trap and served as a rain cover and to minimize capture of plant debris and airborne arthropods.

Traps were run during four consecutive days once every four weeks beginning three weeks after the emergence of maize plants and continuing up to maize harvest. Trap contents were pooled within plots and washed in a mesh sieve. The organisms were sorted and preserved in glass vials using 70% alcohol. Beetles were identified to family level but spiders were not identified further before they were counted and recorded for each plot. Identification of specimens was limited to this coarse level by the poor understanding of the fauna and the inadequate taxonomic infrastructure presently available for East Africa.

5.2.3 Data Analysis

Data collected were pooled for individual plots during each cropping season, and analyzed by two-way (treatments x seasons) analysis of variance (ANOVA) (PROC GLM, SAS Institute, 1985) both on actual and log transformed data. Thereafter, pre-planned orthogonal comparisons were made to test for effects of, plant species, intercropping, weeds and mulch. Regression analysis (PROC REG, SAS Institute, 1985) was used to test for linear and quadratic relationships between plant spacing and beetle and spider abundance. Overall population patterns of ground dwelling arthropods over seasons were compared by plotting pooled data for spiders and five numerically dominant beetle families captured during each season. These were standardized to the same number of samples by dividing by the number of samples taken within the respective season. Data obtained represented the average number of captures per trapping period.

5.3 RESULTS

5.3.1 Abundance of ground-dwelling beetles and spiders

The mean activity abundance of ground-dwelling beetles was lowest in the maize and leucaena monocrop plots, and highest in the 2.25m intercropped plot (Figure 5.1a). However, neither the overall ANOVA or the pre-planned contrasts detected significant differences among treatments (Figure 5.1a and Table 5.1a). Pattern of mean activity of spiders was similar to that of beetles, but again differences among treatments were not significant in view of the relatively large variances (Figure 5.1b and Table 5.1b). When beetles were partitioned into three trophic groups based on a generalized assessment of feeding habits prevailing in the included families (predators, herbivores and detritivores), there were still no statistically significant differences among treatments except the maize monocrop plots which had significantly fewer predatory beetles than the leucaena monocrop plots (Figures 5.2 a, b & c and Tables 5.2 a, b & c).

A total 4365 ground-dwelling beetles belonging to some 18 families were collected over the four cropping seasons of sampling. Among these, five families (Carabidae, Elateridae, Scarabaeidae, Staphylinidae and Tenebrionidae) each accounting for over 10% of the beetles collected, were the most abundant beetle groups. Collectively, these families accounted for 74% of all beetles, with the Carabidae being the most numerous and representing 21.1% of the catches (Table 5.3). During the same period, some 1291 spiders were also captured.

Analyses of beetle abundance patterns over seasons (Figure 5.3) shows that during the first season of trapping (long rains, 1993), the Scarabaeidae were the most common accounting for 67.5% of the beetles captured while the Carabidae accounted for only 3.5%. However, by the fourth trapping season, capture rate of Scarabaeidae had fallen considerably. On the other hand, abundance of Carabidae had risen by over forty fold, making them the most common beetle family group during both seasons of 1994. Captures of the Elateridae and Staphylinidae also increased considerably over the period of the study.

Generally, there was a relative increase in the number of beetles caught over time (Figure 5.3), though this was not true between the short rains of 1993 and the long rains of 1994. Similarly, spider activity-abundance patterns also increased both consistently and considerably in the numbers captured over the period of the study (Figure 5.3).

5.4 DISCUSSION

In this study, I could not demonstrate significant effects of vegetation structure on the activity and abundance of soil inhabiting beetles and spiders, a finding similar to that repeated for other comparisons of these taxa between monocultures and polycultures (Purvis and Curry, 1984; Chiverton and Sotherton, 1991; Ali and Reagan, 1986). Thus, spiders which were presumed to be entirely predatory, provided little evidence for the operation of the enemies hypothesis. On the other hand, responses to either the enemies or

resource concentration hypotheses by beetles may have been confounded by their diverse and conflicting trophic groupings.

When beetles were partitioned into three trophic groups, it was evident that the leucaena monocrop plot attracted significantly more predatory families than the maize monocrop. The leucaena monocrop plot had the highest density of uninterrupted leucaena plants. Thus, the predators most of which are generalists, were attracted by the uninterrupted supply of psyllid prey in the leucaena monocrop plots and least attracted by the maize monocrop, which did not have a comparable continuous supply of prey. On the other hand, the leucaena monocrop plot seemed to attract fewer herbivorous and detritivorous families, though these trends were not statistically significant. Nonetheless, this may weakly suggest that, leucaena being an introduced tree species, is probably less utilized by herbivores, and when planted as a monocrop, may also provide a less diverse food base than required by many detritovores. This conjecture is consistent with reports that ground-dwelling detritivores and herbivores are more abundant in weedy and therefore vegetationally diverse habitats with a greater variety of food sources (e.g. Purvis and Curry, 1984).

The beetle community structure in my study revealed that the Carabidae, which are generally characterized as predators of soil- and litter-inhabiting insects, were the most common beetle group. Information about beetle community structure in tropical African agroecosystems is scarce. However, a survey of soil insects in groundnut fields in southern Africa reported the predominance of Scarabaeidae in areas of intensive agriculture, over 1000mm of rainfall a year, with sandy or loamy soils (Wightman and Wightman, 1994). Alike my study, various elaterids and tenebrionids were also relatively abundant, particularly in Malawi. However, their study was selective and specific to herbivorous insects associated with groundnuts.

There was a general increase in the number of beetles and spiders captured over the period of my study. Spectacular increases were observed among the carabids, elaterids, staphylinids and spiders, although captures of scarabs decreased over the same

period. Comparable data from the immediate neighbourhood that would assist in making generalizations about the observed trends is lacking for my studies. This could have been achieved by setting control traps in situations representing the huge maize monocultures that is the present cropping alternative for the coastal landscape, and in the unmanaged or natural habitat surrounding the experimental field. Nonetheless, other workers have similarly reported changes in abundance and species richness of ground beetles resulting from differing farm management strategies (Dritschilo and Wanner, 1980; Cárcamo et al., 1995). Moreover, some beetle groups such as the Carabidae, have been proposed to be effective indicators of perturbation in terrestrial communities, and provide important links between trophic levels (Dritschilo and Erwin, 1982). Thus, the increased abundance of most beetle taxa under the cropping system in my studies suggest that alley cropping could assist with conservation of ground dwelling arthropods.

In the tropics, agriculture is often associated with degradation of natural resources through soil erosion, water contamination, deforestation, desertification and loss of productivity (Dover and Talbot, 1987; Brown and Lugo, 1994). Moreover, loss of biodiversity has been frequently associated with unrestricted human use of forests (Wilson, 1988; Silver et al., 1996). Most conservation efforts in the tropics and elsewhere have tended to focus on the preservation of few species of large plants and animals, with little attention to smaller organisms like arthropods, even though they comprise approximately 90% of all species (Pimentel et al., 1992). And yet, some of these arthropods, particularly the ground dwellers studied here, are species involved in nutrient recycling and biological control (Best and Beegle, 1977; Purvis and Curry, 1984; Brust et al., 1986; Robertson et al., 1994), and thus have direct implications for the sustainability of agricultural production. There is need for further development of resource production technologies such as agroforestry that have potential to protect and enhance biodiversity of arthropods.

In general, land areas managed for agriculture, forestry and human settlements harbor large number of species (Pimentel et al, 1992; Western and Pearl 1989). The underlying reason for this may be that such managed systems tend to maximize biomass, and positive correlations between production and species abundance are commonly

recorded (Ward and Lakhani, 1977; Pimentel and Warneke, 1989; Sugden and Rands, 1990). One way of achieving increased biomass in agricultural systems is through intercropping and agroforestry, and these farming systems have been associated with increases in species numbers (Pimentel et al., 1992). It therefore appears that use of such practices promote ecological richness, and that plots managed in these ways may act as natural reservoirs for arthropods and other species. Thus, agricultural practices in densely populated areas of tropical Africa should be modeled to serve purposes of biological conservation because natural habitats in the continent continue to be fragmented and reduced by human activity. Agroforestry, with carefully selected tree species, may ameliorate the effects of habitat loss on invertebrate faunas. Moreover, agroforestry, may even reverse the impacts of some traditional farming practices in tropical Africa like slash and burn agriculture, which is indiscriminately destructive to both flora and fauna.

5. 5 CONCLUSIONS

Alley cropping leucaena with maize did not significantly increase the abundance of ground-dwelling beetles and spiders. Therefore, my studies did not support, either the enemies or the resource concentration hypotheses. On the other hand, overall beetle and spider abundance increased on the plots during the period of these experiments, suggesting a general preference for, and suitability of the maize-leucaena habitat for arthropods. Thus, agroforestry may serve the purpose of biological conservation, particularly in areas affected by impacts of land-based resource utilization. Improved support for taxonomic infrastructure and studies to increase knowledge about the ecology and resource utilization by various insect taxa will be useful for future studies in tropical African agroecosystems.

5.6 REFERENCES

Ali, A. D. and T. E. Reagan. (1986). Influence of selected weed control practices on araneid faunal composition and abundance in sugarcane. Environ. Entomol. 15: 527-537.

Andow, D. A. 1983a. Plant diversity and insect populations in experimental agroecosystems: interactions among beans, insects and weeds. Ph.D. dissertation, Cornell University, Ithaca, N.Y. 201 pp.

Andow, D. A 1983b. Agricultural crop diversity and insect populations. Chapter 3. *In* D. Pimentel [ed.], Ecological aspects of pest management. Dept. Entomology, Cornell University, Ithaca, N.Y.

Andow, D. A. 1986. Plant diversification and insect population control in agroecosystems, pp. 277-386. *In.* D. Pimentel [ed.], Some aspects of integrated pest management. Dept. Entomology, Cornell University, Ithaca, N.Y.

Andow, D. A. 1988. Management of weeds for insect manipulation in agroecosystems, pp.265-301. *In* M. A. Altieri & M. Liebman, [eds.], Weed management in agroecosystems: ecological approaches. CRC, Boca Raton, Fla.

Andow, D. A. 1991. Vegetational diversity and arthropod population response. Ann. Rev. Entomol. 36: 561-586.

Andow, D. A. and S. J. Risch. 1985. Predation in diversified agroecosystems: relations between a coccinellid predator and its food. J. Appl. Ecol. 22: 357-72.

Best, L. R. and C. C. Beegle. 1977. Food preferences of five species of of carabids commonly found in Iowa cornfields. Environ. Entomol. 6: 9-12.

Brown, S. and A. E. Lugo. 1994. Rehabilitation of tropical lands: a key to sustaining development. Restoration Ecology 2: 97-111.

Brust, G. E., B. R. Stinner and D. A. McCartney. 1986. Predation by soil inhabiting arthropods in intercropped and monoculture agroecosystems. Agric. Ecosystems Environ. 18: 145-154.

Cárcamo, H. A., J. K. Niemala and J. R. Spence. 1995. Farming and ground beetles: Effects of agronomic practice on populations and community structure. Can. Entomol. 127: 123-140

Cárcamo, H. A. and J. R spence. 1994. Crop type effects on the activity and distribution of ground beetles (Coleoptera: Carabidae). Environ. Entomol. 23: 684-692.

Chiverton, P. A. and N. Sotherton. 1991. The effects on beneficial arthropods on the exclusion of herbicides from cereal crop edges. J. Appl. Ecol. 28: 1027-1039.

Dover, M. and L. Talbot. 1987. To Feed the Earth - AgroEcology for Sustainability in a Changing World Order. World Resources institute, 122 pp.

Dritschilo, W. and D. Wannar. 1980. Ground beetle abundance in organic and conventional corn fields. Environ. Entomol. 9: 629-631.

Dritschilo, W. and T. L. Erwin. 1982. Response in abundance and diversity of cornfield carabid communities to differences in farm practices. Ecology 63: 900-904.

Herzog, D. C. and J. E. Funderburk. 1986. Ecological bases for habitat management and pest control. *In* M. Kogan (ed.), Ecological theory and integrated pest management practice. Wiley, New York. pp. 217-250.

Luff, M. L. 1987. Biology of polyphagous ground beetles in agriculture. Agric. Zool. Rev. 3: 237-278.

Lund, R. D. and F. T. Turpin. 1977. Carabid damage to weed seeds found in Indiana cornfield Environ. Entomol. 6: 695-698.

Perfecto. I., B. Horwith, J. Vandermeer, B. Schultz, H. McGuinness and A. Dos Santos. 1986. Effects of plant diversity and density on the emigration rate of two ground beetles, *Harpalus pennsylvanicus* and *Evarthrus sodalis* (Coleoptera: carabidae, in a system of tomatoes and beans. Environ. Entomol. 15: 1028-1031

Pimentel, D. and A. Warneke. 1989. Ecological effects of manure, sewege sludge and other organic wastes on arthropod populations. Agr. Zool. Rev. 3: 1-30.

Pimentel, D., U. Stachow, D. A. Takacs, H. W. Brubaker, A. R. Dumas, J. J. Meaney, J. A. S. O'Neil, D. E. Onsi and D. B. Corzilius. 1992. Conserving biological diversity in agricultural/forestry systems. BioScience 42: 354-362.

Potts, G. and G. P. Vickerman. 1974. Studies on the cereal ecosystems. Adv. Ecol. Res. 8: 107-197.

Purvis, G. and J. P. Curry. 1984. The influence of weeds and farmyard manure in the activity of carabidae and other ground-dwelling arthropods in sugar beet root crop. J. appl. Ecol. 21: 271-283.

Risch, S. J. 1980. The population dynamics of several herbivorous beetles in tropical agroecosystem: the effect of intercropping corn, beans, squash in Costa Rica. J. Appl. Ecol. 17: 593-612.

Risch, S. J. 1981. Insect herbivore abundance in tropical monocultures and polycultures: An experimental test of two hypotheses, Ecology 62: 1325 - 1340.

Risch, S. J., D. Andow, and M. A. Altieri. 1983. Agroecosystem diversity and pest control: Data, tentative conclusions, and new research directions. Environ. Entomol. 12: 625-629.

Robertson, L. N., B. A. Kettle and G. B. Simpson. 1994. The influence of tillage practices on soil macrofauna in semi-arid agroecosystem in northeastern Australia. Agric. Ecosystems environ. 48: 149-156.

Root, R. B. 1973. Organization of plant - arthropod association in simple and diverse habitats: The fauna of collards (*Brassicae olevaceae*). Ecol . Monogr. 43: 95-124.

Russell, E. P. 1989. Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. Environ. Entomol. 18: 590-599.

Sheehan, W. 1986. Response by specialist and generalist natural enemies to agroecosystem diversification: a selective review. Environ. Entomol. 15: 456-461.

Silver, W. L., S. Brown and A. E. Lugo. 1996. Effects of changes in biodiversity on ecosystem function in tropical forests. Conservation Biology 10: 17 - 24.

Statistical Analysis Systems Institute Inc. 1985 SAS Users Guide. Statistics, Version 5 edn. SAS Institute Inc., Cary, NC.

Sugden, A. M. and G. F. Rands. 1990. The ecology of of temperate cereal fields. Trends Ecol. Evol. 5: 205-206.

Thiele, H. 1977. Carabid beetles in their environments. Springer, New York.

Vandermeer, J. H. 1990. Intercropping. *In* C.R. Carrol, J. H. Vandermeer and P. M. Rosset (eds.), Agroecology. McGraw Hill, New York. pp. 481-516.

Ward, L. K. and K. H. Lakhani. 1977. The conservation of juniper: the fauna of food-plant island sites in southern England. J. Appl. Ecol. 14: 121-135.

Western, D. and M. C. Pearl. 1989. Conservation for the Twenty-first Century. Oxford University Press, New York.

Wightman, J. A. and A. S. Wightman. 1994. An insect, agronomic and sociological survey of groundnut field in southern Africa. Agric. Ecosystems Environ. 51: 311-331.

Wilson, E. O. 1988. Biodiversity. National Academy Press, Washington, D.C.

Winder, L. 1990. Predation of the cereal aphid *Sitobion avanae* by polyphagous predators on the ground. Ecol. Entomol. 15: 105-110.

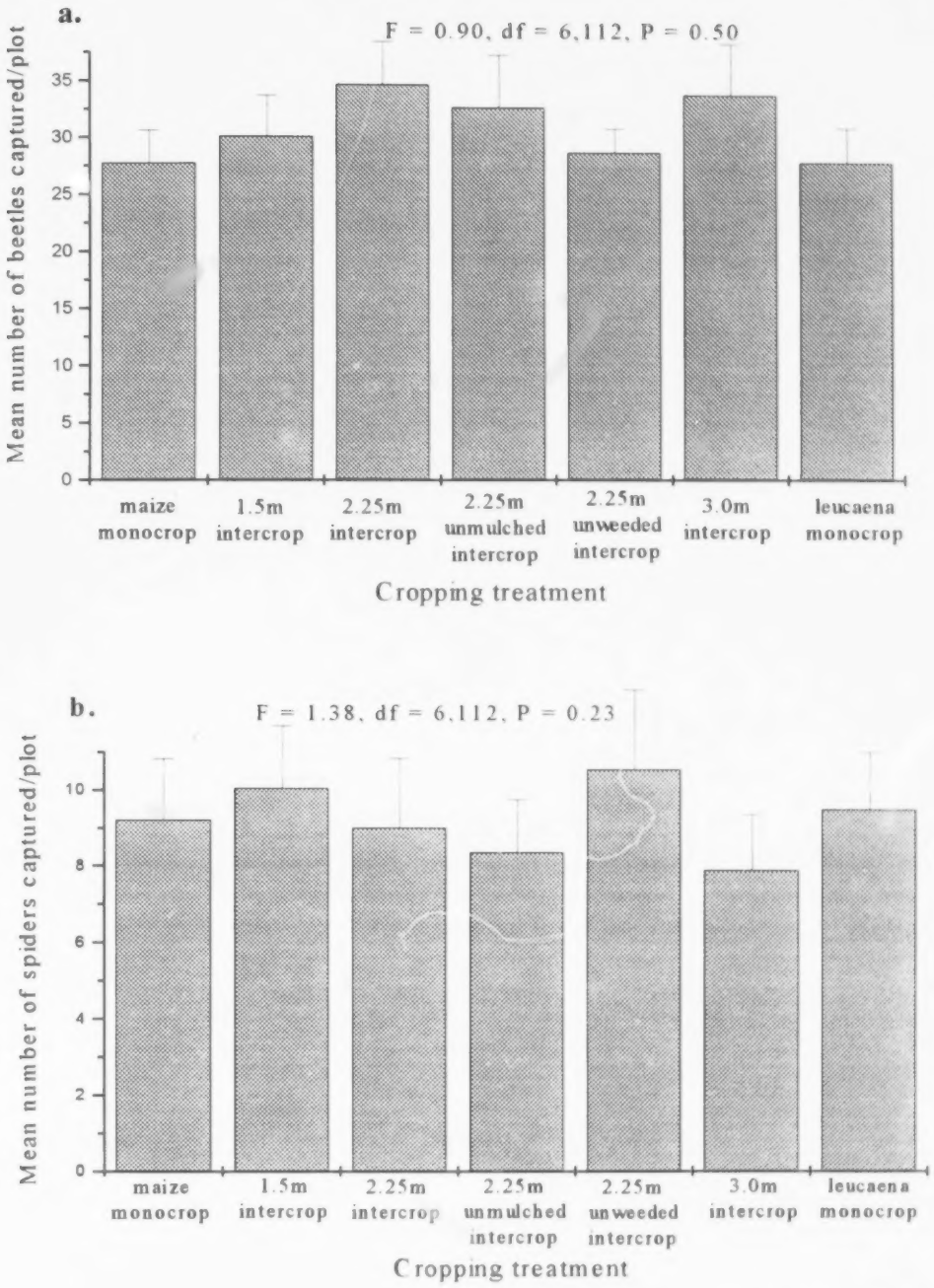


Figure 5.1. Average (±SE) pitfall trap captures for epigaeic arthropods at Mtwapa. Means represent treatment averages over four cropping seasons. a. ground dwelling beetles, b. ground dwelling spiders.

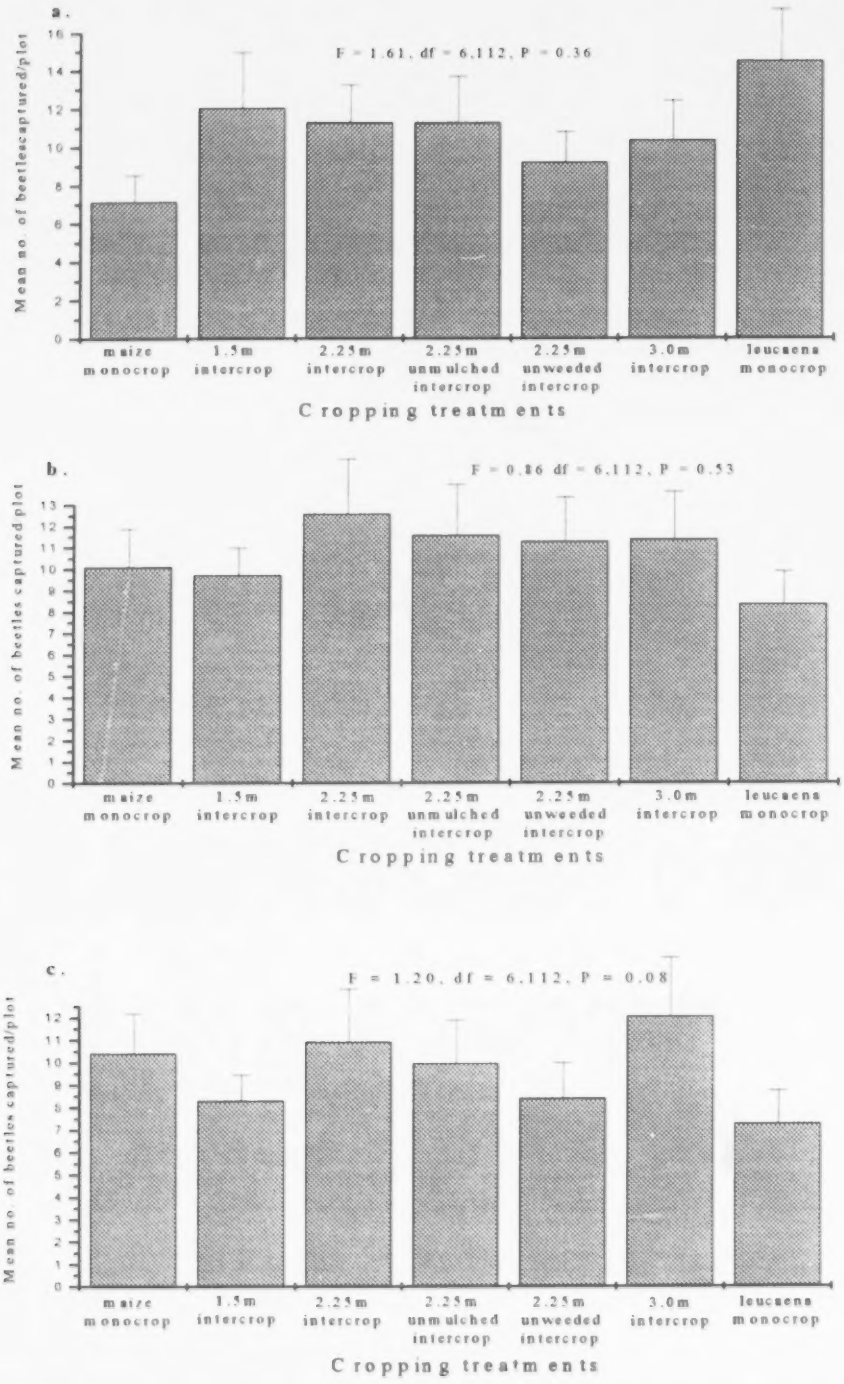


Figure 5.2. Average (±SE) pitfall trap captures for epigaeic beetles at Mtwapa. Means represent treatment averages over four cropping seasons. a. predatory b. detrivorous c. herbivorous

Figure 5.3: Relative abundance of beetles and spiders per cropping season at Mtwapa

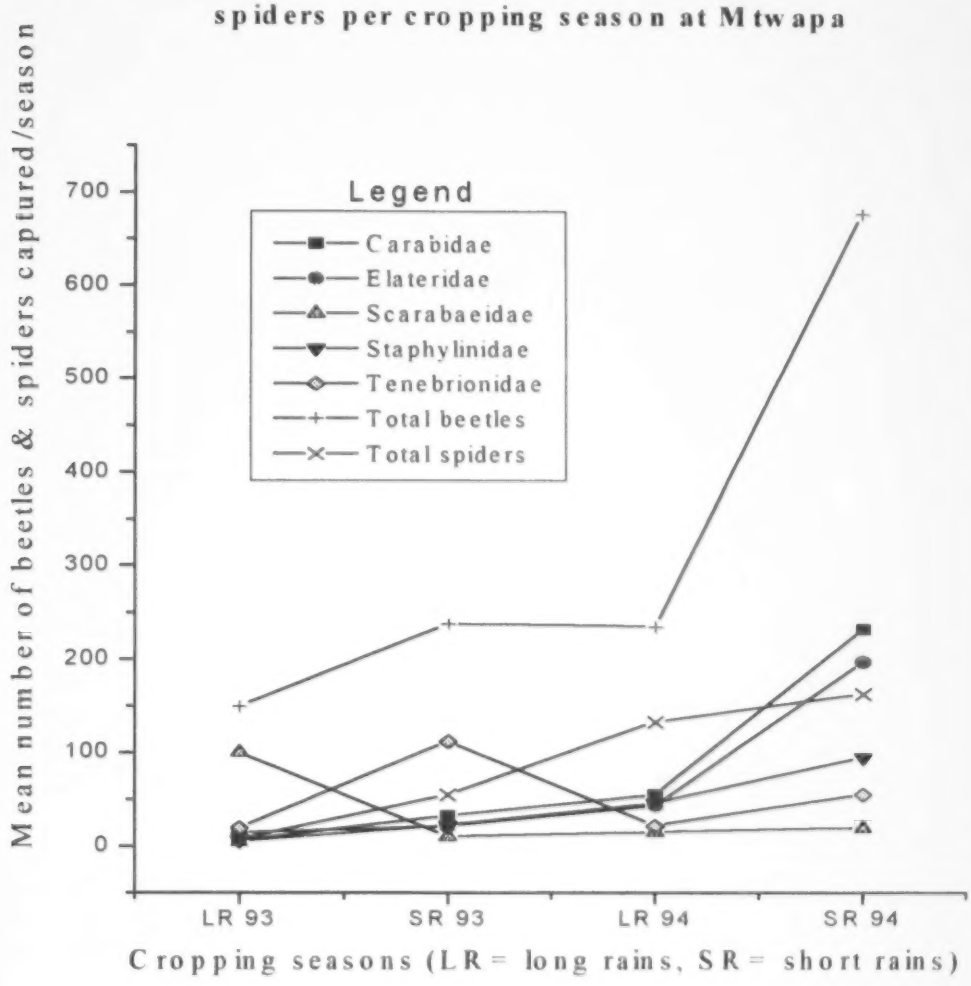


Table 5.1a: Orthogonal comparisons for mean number of beetles captured per plot at Mtwapa

Contrasts	P
maize monocrop vs intercrops	0.20
leucaena monocrop vs intercrops	0.22
maize mono vs leucaena mono	0.96
weeded vs unweeded	0.19
mulched vs unmulched	0.65

Spacing regression analysis	R^2	P
linear	0.034	0.52
quadratic	0.026	0.58

Table 5.1b: Orthogonal comparisons for mean number of spiders captured per plot at Mtwapa

Contrasts	P
maize monocrop vs intercrops	0.97
leucaena monocrop vs intercrops	0.70
maize mono vs leucaena mono	0.79
weeded vs unweeded	0.85
mulched vs unmulched	0.56

Spacing regression analysis	R^2	P
linear	0.006	0.79
quadratic	0.014	0.68

Table 5.2a: Orthogonal comparisons for mean number of predatory beetles per plot at Mtwapa

Contrasts	P
maize monocrop vs intercrops	0.07
leucaena monocrop vs intercrops	0.07
maize mono vs leucaena mono	0.00
weeded vs unweeded	0.36
mulched vs unmulched	1.00

Spacing regression analysis	R^2	P
linear	0.030	0.56
quadratic	0.000	0.98

Table 5.2b: Orthogonal comparisons for mean number of detrivorous beetles per plot at Mtwapa

Contrasts	P
maize monocrop vs intercrops	0.48
leucaena monocrop vs intercrops	0.08
maize mono vs leucaena mono	0.40
weeded vs unweeded	0.67
mulched vs unmulched	0.64

Spacing regression analysis	R^2	P
linear	0.055	0.39
quadratic	0.109	0.23

Table 5.2c: Orthogonal comparisons for mean number of herbivorous beetles per plot at Mtwapa

Contrasts	P
maize monocrop vs intercrops	0.76
leucaena monocrop vs intercrops	0.12
maize mono vs leucaena mono	0.15
weeded vs unweeded	0.26
mulched vs unmulched	0.67

Spacing regression analysis	R^2	P
linear	0.102	0.26
quadratic	0.005	0.81

Table 5.3: Abundance of beetles by Family taxon at Mtwapa

Beetle Family	Numbers	%	Trophic group
Carabidae	920	21.08	Predatory
Chrysomelidae	290	6.64	Herbivore
Elateridae	772	17.69	Herbivore
Histeridae	78	1.79	Detritovore
Nitidulidae	113	2.59	Herbivore
Oedomeridae	134	3.07	Herbivore
Scarabaeidae	563	12.9	Detritovore
Staphylinidae	551	12.62	Predatory
Tenebrionidae	855	19.59	Detritovore
Others	89	2.04	
Total	4365		

6. GENERAL DISCUSSION AND CONCLUSIONS

6.1 SUMMARY, DISCUSSION AND CONCLUSIONS

Vegetational diversity is associated with both the diversity (Murdoch et al., 1972; Root, 1973; Price and Waldbauer, 1975) and stability (Pimental., 1961; Southwood and Way, 1970; van Emden and Williams, 1974) of the herbivore community. Diversity among plant assemblages has been proposed as being the first line of host plant defense against potential insect pests (Speight and Lawton, 1976.). Reductions of pest incidence in diverse vegetation may be the result of a complex of factors like increased parasitoid and predator populations, availability of alternative food for natural enemies, decreased colonization and reproduction of pests, chemical repellency, masking and /or emigration and optimum synchrony between pests and natural enemies (Matteson et al., 1984). Vandermeer (1990) has summarized the mechanisms believed to operate in reducing pest attack in vegetationally diverse ecosystems in three general hypotheses, namely (1) the resource concentration or disruptive-crop hypothesis, (2) the enemies hypothesis and, (3) the trap-crop hypothesis. These hypotheses have been reviewed in Chapters 1, 2 and 3.

Vegetational diversity can be increased in agroecosystems through practices such as multiple cropping and agroforestry. Agroforestry has been frequently suggested as a means of reversing negative impacts of land use (Lundgren and Raintree, 1982; Odhiambo, 1990) prevalent in tropical Africa (Dover and Talbot 1987). As reported in this thesis, my studies, conducted at Mtwapa in coastal Kenya and Amoyo in western Kenya, tested the explanatory power of the resource concentration hypothesis and the enemies hypothesis in the maize-leucaena agroforestry system. I sought to evaluate the effect of this cropping system on the insect fauna relevant to production, and to establish if this system has pest management benefits.

In Chapter 2, I have explored how effect of alley cropping leucaena with maize under varying spatial arrangements and/or cultural influences the host finding, colonizing ability and abundance of stem boring lepidopterans, the principal pests of maize in East

Africa. An assessment of damage levels and yield losses caused by these pests is also included. Alley cropping leucaena with maize reduced insect pest infestation, abundance and damage on the maize crop by stem borers. Thus, my results for this cropping system supported the resource concentration hypothesis, like several other studies (reviewed by Andow, 1991). Furthermore, the reduced pest numbers translated into increased yields, the ultimate goal of any crop production system. However, in Chapters 4 and 5, which examined the effect of resource concentration on populations of the leucaena psyllid and ground-dwelling beetles respectively, the hypothesis was not supported. This finding is also consistent with other studies (reviewed by Andow, 1983, 1986, 1988, 1991 and Risch et al., 1983). I concluded that maize stem borers can be reduced by the maize-leucaena vegetation structure, while the leucaena psyllid and herbivorous and detrivorous ground - dwelling beetles were not. Thus, the herbivores examined in my studies responded differently to the resource concentration hypothesis. This is consistent with reports that responses to this hypothesis may vary enormously among plant combinations (Kareiva, 1983).

In Chapters 3-5, I examined the possible implications of the enemies hypothesis for insect pests and epigaeic arthropods in the maize-leucaena agroforestry system. Chapter 3 deals mainly with specialist parasitoids and general predation of maize stem borers, while Chapters 4 and 5 tested predictions of the hypothesis for above ground predatory ladybird beetles associated with the psyllid and ground-dwelling predatory beetles within the cropping system respectively. The maize-leucaena cropping system did not increase, and in fact even reduced the abundance and/or activity of some natural enemies of maize stem borers more than in the maize monocrop. The number of ladybirds and ground-dwelling beetles did not differ significantly between treatments at Mtwapa. Thus, the enemies hypothesis that natural enemies will be more abundant in polycultures than in monocultures (Root, 1973) was not corroborated. Within the spatial and temporal scale of my studies, the maize-leucaena agroforestry system did not increase the abundance and activity of natural enemies (specialist or generalist) of maize stem borers, psyllids, and other insects. This conclusion agrees with studies (reviewed by Russell, 1989 and Andow,

1991) which have reported variable responses of natural enemies to the hypothesis. Presently there is no theory that predicts when natural enemies will exert significant mortality in polycultures (Andow, 1991).

In my studies on the maize-leucaena system, resource concentration seemed to be responsible for reduced abundance and activity of maize stem borers. On the other hand, the associated effect on natural enemies may in some cases act antagonistically to resource concentration. In this respect, my work supports similar conclusions about polycultures by Andow and Risch (1985, 1987) and stands in contrast to reports that these two hypotheses invoke complementary mechanisms (Russell, 1989). Nonetheless, the reduction in pest abundance in my studies translated into an overall yield advantage. Therefore, this agroforestry system can be recommended for crop protection and production of food and fiber in East Africa, particularly in situations where maize stem bores are a significant problem.

The faunistic studies presented in Chapter 5 show that abundance of ground-dwelling beetles and spiders increased on the plots during the period of these experiments. The two monocrops had consistently lower incidence of both beetles and spiders, while the unweeded plot had highest incidence of spiders. However, these differences were statistically insignificant. A pragmatic approach towards explaining these trends could have been achieved by setting control traps in situations representing the huge maize monocultures that is the present cropping alternative for the coastal landscape. Nonetheless, my results weakly suggest that vegetational diversity may be correlated with abundance of insect populations.

My findings are consistent with reports that cropping systems that increase biomass, such as multiple cropping and agroforestry, are associated with increases in species numbers (Pimentel et al., 1992). Thus, for tropical Africa, where agriculture has often been associated with degradation of natural resources (Dover and Talbot, 1987; Brown and Lugo, 1994), including loss of biodiversity (Wilson, 1988; Silver et al., 1996), agroforestry may serve the purpose of biological conservation, particularly in areas

affected by impacts of land-based resource utilization. Moreover, some of these arthropods, particularly the ground dwellers studied here, are probably involved in nutrient recycling and biological control (Best and Beegle, 1977; Purvis and Curry, 1984; Brust et al., 1986; Robertson et al., 1994), and thus have direct implications for the sustainability of agricultural production. This is a highly desired goal for tropical Africa where farmers are resource-limited and cannot afford expensive agrochemicals to otherwise sustain productivity.

Leucaena is a highly suitable tree species for agroforestry in tropical Africa and is presently used extensively for various products and services (NAS, 1980,1984). However, the increasing use of leucaena for agroforestry is threatened by the leucaena psyllid, a pest new to Africa. Studies about local population dynamics are prerequisite in developing effective management strategies for any pest species. My studies on the population dynamics of the psyllid as reported in Chapter 4, showed that populations were influenced by weather, particularly rainfall, and availability of suitable shoots. New growth of young shoots following rainfall, encouraged psyllid abundance as long as weather conditions were not extreme. Furthermore, damage to leucaena appears to represent the cumulative and interactive effect of both the feeding activity of psyllids and prevailing environmental/climatic conditions, and does not closely track the actual population of and/or damage by psyllids at a given time. Psyllid populations were generally much higher at Mtwapa than at Amoyo, suggesting environmental constraints on population growth. Moreover, damage to leucaena plants in the highlands was almost insignificant, as compared to the impact of the psyllid in coastal Kenya. Thus, leucaena may be more viable for agroforestry in the interior where no control interventions against the psyllid are presently required.

6. 2 FUTURE STUDIES

My studies are only a beginning and provide a basis for recommendations about future research. The response of leucaena psyllid to both the resource concentration and enemies hypotheses should be studied further. I believe that results of my studies may have been confounded by the general spatial arrangement of leucaena plants, and the apparent lack of temporal control for both hypotheses. Spacing of leucaena plants allowed some form of contact between plants within rows, and in cases between hedgerows. This would have confounded responses to both hypotheses based on dispersal patterns of the herbivore and its natural enemies. Temporally, the psyllids were actually exposed to a monocrop after harvesting of the maize intercrop, thus reducing the effect of treatments. More reliable results may be obtained if host plants are more completely isolated by more effective use of non host plants as barriers. Alternating leucaena with another desirable/adaptable tree species within or between hedgerows could be another practical alternative that would test either hypothesis against the crop pests and the psyllid, while increasing, and also maintaining diversity after crop harvest.

Because there is no present theory that predicts when natural enemies will exert significant mortality in polycultures, subsequent studies of the enemies hypothesis should address the possible effects of multitrophic interactions, and the influence of interceding abiotic factors within each system. The information thus generated may lead to a better understanding of the relative importance of various factors that control enemy populations, responses and effectiveness in polycultures, and move us towards a more predictive general theory of enemy activity in diverse systems.

Understanding of the leucaena psyllid in tropical Africa is still at a relatively low level. In the future, field life table studies will be necessary to more fully determine the role of both biotic and abiotic factors on psyllid populations, and to establish the basis of major differences in population regulation between sites, like those observed at Amoyo and Mtwapa. This will allow predictions about psyllid populations and subsequent plant

damage to support site-specific recommendations about use and adoption of leucaena as an agroforestry tree species.

Finally, as suggested in my studies, agroforestry appears to have great potential in biological conservation, particularly in areas affected by impacts of land-based resource utilization. Therefore, more studies should be focused on the invertebrate fauna associated with this cropping system *vis-à-vis* the surrounding habitats, and a better understanding of the ecology and resource utilization by various taxa within the system. This will require improved support for taxonomic infrastructure within the region.

6.3 REFERENCES

Andow, D. A. 1983. Plant diversity and insect populations in experimental agroecosystems: interactions among beans, insects and weeds. Ph.D. dissertation, Cornell University, Ithaca, N.Y. 201 pp.

Andow, D. A. 1986. Plant diversification and insect population control in agroecosystems, pp. 277-386. *In.* D. Pimentel [ed.], Some aspects of integrated pest management. Dept. Entomology, Cornell University, Ithaca, N.Y.

Andow, D. A. 1988. Management of weeds for insect manipulation in agroecosystems, pp.265-301. *In* M. A. Altieri & M. Liebman, [eds.], Weed management in agroecosystems: ecological approaches. CRC, Boca Raton, Fla.

Andow, D. A. 1991. Vegetational diversity and arthropod population response. Annu Rev. Entomol. 36: 561-586.

Andow, D. A. and S. J. Risch. 1985. Predation in diversified agroecosystems: relations between a coccinellid predator and its food. J. Appl. Ecol. 22: 357-72.

Andow, D. A. and S. J. Risch. 1987. Parasitism in diversified agroecosystems: Phenology of *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) Entomophaga 32: 255-260

Best, L. R. and C. C. Beegle. 1977. Food preferences of five species of carabids commonly found in Iowa cornfields. Environ. Entomol. 6: 9-12.

Brust, G. E., B. R. Stinner and D. A. McCartney. 1986. Predation by soil inhabiting arthropods in intercropped and monoculture agroecosystems. Agric. Ecosystems Environ. 18: 145-154.

Dover, M. and L. Talbot. 1987. To Feed the Earth - AgroEcology for Sustainability in a Changing World Order. World Resources institute, 122 pp.

Kareiva, P. M. 1983. Patchiness, dispersal and species interactions: Consequences for communities of herbivore insects. *In.* J. Diamond and T. Case (eds.), Community ecology, Harper and Row, New York, pp.192-206.

Lundgren, B. O. and J. B. Raintree. 1982. Sustained agroforestry. *In* B. Nestel (eds.), Agricultural research for development: Potentials and challenges in Asia. ISNAR, The Hague, pp. 37-49.

Matteson, P. C., M. A. Altieri and W. C. Gagne. 1984. Modification of smaller farmer practices for better management. Annu. Rev. Entomol. 29: 383-402.

Murdoch, W. M., F. C. Evans and C. H. Peterson. 1972. Diversity and pattern in plants and insects. Ecology 53: 819-829.

NAS. 1980. Firewood Crops: shrubs and tree species for energy production. National Academy of Sciences, Washington, D.C. 237pp.

NAS. 1984. Leucaena: Promising Forage and Tree Crop for the Tropics. Innovations in Tropical Reforestation; Second Edition, National Academy Press, Washington, D.C. 100pp.

Odhiambo, T. R. 1990. Assets for an IPM specialist with particular reference to *Chilo*. Insect Sci. Application Vol. 11, No. 4/5, pp. 571-576.

Pimentel, D. 1961. Species diversity and insect population outbreaks. Ann. Ent. Soc. Am. 54: 76-87.

Pimentel, D., U. Stachow, D. A. Takacs, H. W. Brubaker, A. R. Dumas, J. J. Meaney, J. A. S. O'Neil, D. E. Onsi and D. B. Corzilius. 1992. Conserving biological diversity in agricultural/forestry systems. BioScience 42: 354-362.

Price, P. W. and G. P. Waldbauer. 1975. Ecological aspects of pest management. *In* R. L. Metcalf and W. H. Luckman (eds.), Introduction to insect pest management. John Wiley and Sons, New York, pp. 37-73.

Purvis, G. and J. P. Curry. 1984. The influence of weeds and farmyard manure in the activity of carabidae and other ground-dwelling arthropods in sugar beet root crop. J. appl. Ecol. 21: 271-283.

Risch, S. J., D. Andow, and M. A. Altieri. 1983. Agroecosystem diversity and pest control: Data, tentative conclusions, and new research directions. Environ. Entomol. 12: 625-629.

Robertson, L. N., B. A. Kettle and G. B. Simpson. 1994. The influence of tillage practices on soil macrofauna in semi-arid agroecosystem in northeastern Australia. Agric. Ecosystems Environ. 48: 149-156.

Root, R. B. 1973. Organization of plant - arthropod association in simple and diverse habitats: The fauna of collards (*Brassicae olevaceae*). Ecol . Monogr, 43: 95-124.

Russel, E. P. 1989. Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. Environ. Entomol. 18: 590-599.

Silver, W. L., S. Brown and A. E. Lugo. 1996. Effects of changes in biodiversity on ecosystem function in tropical forests. Conservation Biology 10: 17 - 24.

Southwood, T. R. E. and M. J. Way. 1970. Ecological background to pest management. *In* R. L. Rabb and F. E. Guthrie, (eds.), Concepts of pest management, North Carolina State University, Raleigh, pp. 6-28.

Speight, M. R. and J. H. Lawton. 1976. The influence of weed cover on the mortality imposed on artificial prey by predatory ground beetles in cereal fields. Oecologia (Berl.) 23: 211-233.

Vandermeer, J. H. 1990. Intercropping. *In* C. R. Carrol, J. H. Vandermeer and P. M. Rosset (eds.), Agroecology. McGraw Hill, New York. pp. 481-516.

van Emden, H. F and G. C. Williams. 1974. Insect stability and diversity in agroecosystems. Annu. Rev. Entomol. 19: 455-475.

Wilson, E. O. 1988. Biodiversity. National Academy Press, Washington, D.C.